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Notes on Micronesian Pteridophyta, III. Ophioglossum nudicaule in the Caroline Islands[1]

F. R. FOSBERG*

The rather saline environment of a coral atoll seems scarcely the place to look for a terrestrial *Ophioglossum,* and none has heretofore been reported from any atoll to the best of my knowledge. *Ophioglossum pendulum* L., an epiphytic species, has been found on Mili, Namorik, Ebon, and Jaluit atolls, in the southern Marshall Islands (St. John, Occ. Pap. Bishop Mus. **17:** 177–182. 1943; Stone, Micronesica **1:** 155. 1964; Fosberg & Sachet, Atoll Res. Bull. **92:** 2. 1962).

Hence, my astonishment was great when I spotted a small colony of one of these diminutive plants along a path in a coconut plantation just outside a village while I was hurrying to be picked up by a small boat on Fassarai Islet, Ulithi Atoll, August 17, 1965. I stopped, verified the observation, and hastily collected a few specimens (*Fosberg & Evans 47400,* MICH, UH, US).

Two relatively recent papers treat the genus *Ophioglossum* in the Pacific region (Clausen, Mem. Torrey Bot. Club. **19**(2): 1–177. 1938; Wieffering, Blumea **12:** 321–337. 1964). The viewpoints and characters used by these authors are very different, and the keys of neither of them work very readily on the Ulithi specimens. However, after studying very carefully the material and the descriptions, as well as specimens from elsewhere, I conclude that the plants seem to fall, according to both treatments, into *Ophioglossum nudicaule* L. f.

The specimens are very slender and delicate, to over 12.5 (usually 8–10) cm tall, with the blade at most 17 × 12 mm, attached 8–20 mm from the base of the stipe, elliptic to broadly ovate or almost orbicular, sessile, acute to almost truncate at the base, acutish to more usually obtuse to rounded and slightly apiculate at apex, very thin, rather coarsely areolate by rather prominent veins, the areolae becoming smaller and more isodiametric toward the margins, some of them divided by thinner veins into 2 or 3 smaller areolae, or containing 1 or 2 free-ending veins, the marginal cells mostly irregularly elongate parallel with the entire margins, the main basal veins 6–8; in *Fosberg & Evans 47400* 0 (rarely 1 or 2) sterile fronds from the rhizome, these with the stipes about equalling the elliptic, oval, or oboval blades; peduncle to 10.5 cm, usually 6-8 cm, spike 8-16 mm long including the sterile, apical portion, 1.5 mm wide including the sporangia, the sterile portion of the axis between the sporangia 0.2 mm or less wide, sterile apical part, if uninjured, 1-2 mm long, subulate.

An attempt to place this population in one of the varieties recognized by Clausen failed. The plants range in size from small, as in var. *nudicaule* (var. *typicum* of Clausen), to almost the maximum for var. *grandifolium.* Small plants could fit var. *minus.* The blade is the wrong shape for var. *laxum* or var. *tenerum,*

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[1] Number I in this series was in the Amer. Fern J. **40:** 132–147. 1950; number II was in the Amer. Fern J. **48:** 35–39. 1958.

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too small for var. *grandifolium,* the peduncle too long for var. *nudicaule;* the areolae are too long for var. *laxum,* more like those of var. *grandifolium,* to which the plant runs in the key.

This situation supports Wieffering's disregard of all but one of Clausen's varieties, so far as characters of one population could be said to do this. It will be interesting to find out how other atoll populations, if any are found, fit this pattern. Collectors on the wetter coral islands, especially in the western Pacific, should watch for colonies of this species. It has been found on Guam *(Wagner 3700,* US). The plants of this collection are much smaller and have smaller, thicker blades than the Ulithi material; they were identified as var. *tenerum* by Clausen. *Ophioglossum reticulatum* L. has been reported from Palau, Yap, and Truk by previous authors, but I have not seen the material.

REVIEW

"ENDEMIC AREAS IN FERNS," by Rolla Tryon, Biotropica 4: 121–131. 1972.—Phytogeography is an important and often neglected study with respect to the pteridophytes, especially as it relates to the evolution of "geographical species" that form because of spatial isolation. In contrast to the flowering plants, the pteridophytes make ideal subjects for phytogeographic studies because they are fairly equivalent in dispersal capacity. Tryon's study is based primarily on 444 neotropical species in 12 well-monographed genera. Five of the genera are Adiantoids, two each are Cyatheaceae and Polypodiaceae, and one each are Schizaeaceae, Lindsaeaceae, and Pteridaceae. (This, in my estimation, is the only weak point in the analysis: entire families are not present and the sample includes only about 11% of the New World's ferns.) Of the 444 species, 404 are continental, at least in part. The endemics among the continental species are found primarily in the Mexican, Andean, and South Brazilian centers, which have 47%, 39% and 44% endemics, respectively. The Central American and Guayana Highlands centers are secondary and have 12% and 30% endemics, respectively. The areas between the centers have between 0% and 7% endemics. Some endemic genera (e.g., *Pterozonium* and *Doryopteris)* are largely confined to certain rocks and soils derived from them. The affinity of the various pairs of regional centers (i.e., the number of species in common divided by the total number of species less those in common) is directly correlated with the distance between the centers. About a quarter of the 404 continental species have ranges of 300 miles or less; nearly half have ranges of 750 miles or less. A third of them range from 750 to 3000 miles and a sixth range over 3000 miles. The range of apogamous races of some species greatly exceeds that of their parent, sexual races. Large range disjuncts (over 1000 miles) occur in only 112 of the 404 species, and only a third of the vicarious pairs of species are more than 450 miles disjunct. The primary and secondary regional centers are long-time areas of species migration, establishment by long-distance dispersal, and speciation. The intervening areas were or are relatively inhospitable for ferns. This important paper deserves several careful readings and much thought from all who are interested in the phytogeography and evolution of the pteridophyta.—D.B.L.

A Redefinition of the Genus Hemionitis[1]

JOHN T. MICKEL*

In the summer of 1971 during field work on the ferns of the state of Oaxaca, Mexico, I collected four species of the genus *Hemionitis,* only one of which had previously been reported from that state. A broader examination of the genus was undertaken in order to determine the species' limits and relationships. Spore studies showed that certain species of *Hemionitis* had spores that closely resembled those of some species of the closely allied *Gymnopteris,* and so the study was broadened to include the species of both genera.

Hemionitis L. (1753) is typified by *H. palmata* (Underwood, 1899, p. 254) *(Fig. 12),* a species which ranges from Mexico to northern South America and the West Indies. Linnaeus included in *Hemionitis* ferns with so-called "gymnogrammoid sori" (those which run along the veins and lack an indusium). Many ferns with this type of sorus were placed in the genus *Gymnogramma* by Desvaux (1811, p. 304) and more extensively by Hooker and Baker (1868), but gradually species were removed in blocks to such genera as *Pityrogramma, Eriosorus, Bommeria, Anogramma,* and *Gymnopteris.*

The genus *Hemionitis* as commonly construed today includes the widespread *H. palmata, H. pinnatifida* (southern Mexico to Costa Rica; *Fig. 6), H. levyi* (southern Mexico to Costa Rica; *Fig. 7), H. elegans* (southwestern Mexico; *Fig. 5), H. smithii* (Jamaica; *Fig. 10),* and *H. arifolia* (southeastern Asia; *Fig. 6).* The disjunct *H. arifolia* was cause for some concern, and closer examination showed that it also was quite different from the New World species in the scales on the blade, the dark color of the leaf tissue, the more coriaceous texture, the sagittate leaf architecture, the buds at the base of the blade rather than on the margin, and the spores, which have noticeably high ridges, as opposed to the tuberculate spores of *H. palmata.* Thus, there was some justification for establishing a new genus based on *H. arifolia,* but subsequent inclusion of the genus *Gymnopteris* in the study made this hypothesis untenable.

Gymnopteris Bernhardi (1799, p. 297) is based on *Acrostichum rufum* (L.) L. *(= G. rufa* (L.) Bernhardi). In the present study five species of *Gymnopteris* were examined: *G. rufa* (West Indies, Central and northern South America; *Fig. 9), G. tomentosa* (South America; *Fig. 8), G. subcordata* (Mexico to Nicaragua; *Fig. 3), G. vestita* (southeastern Asia; *Fig. 2),* and *G. bipinnata* (southeastern Asia; *Fig. 1). Gymnopteris* is said to differ from *Hemionitis* on the basis of its pinnate architecture and free veins. Other than the pinnate architecture, there are no characters which consistently distinguish the two genera. Other characters contradict the separation of these two genera, and I find a stronger argument for combining the two genera.

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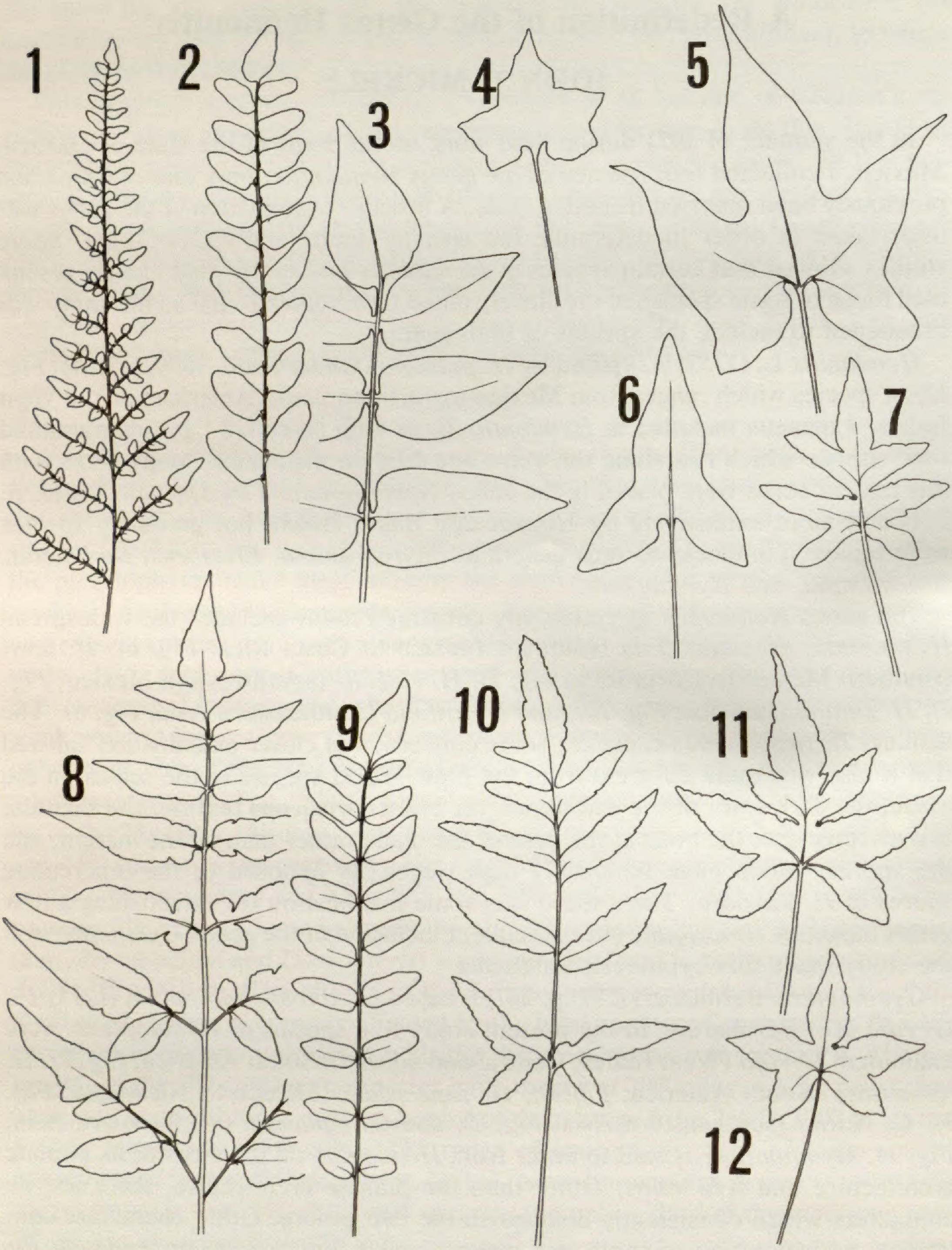
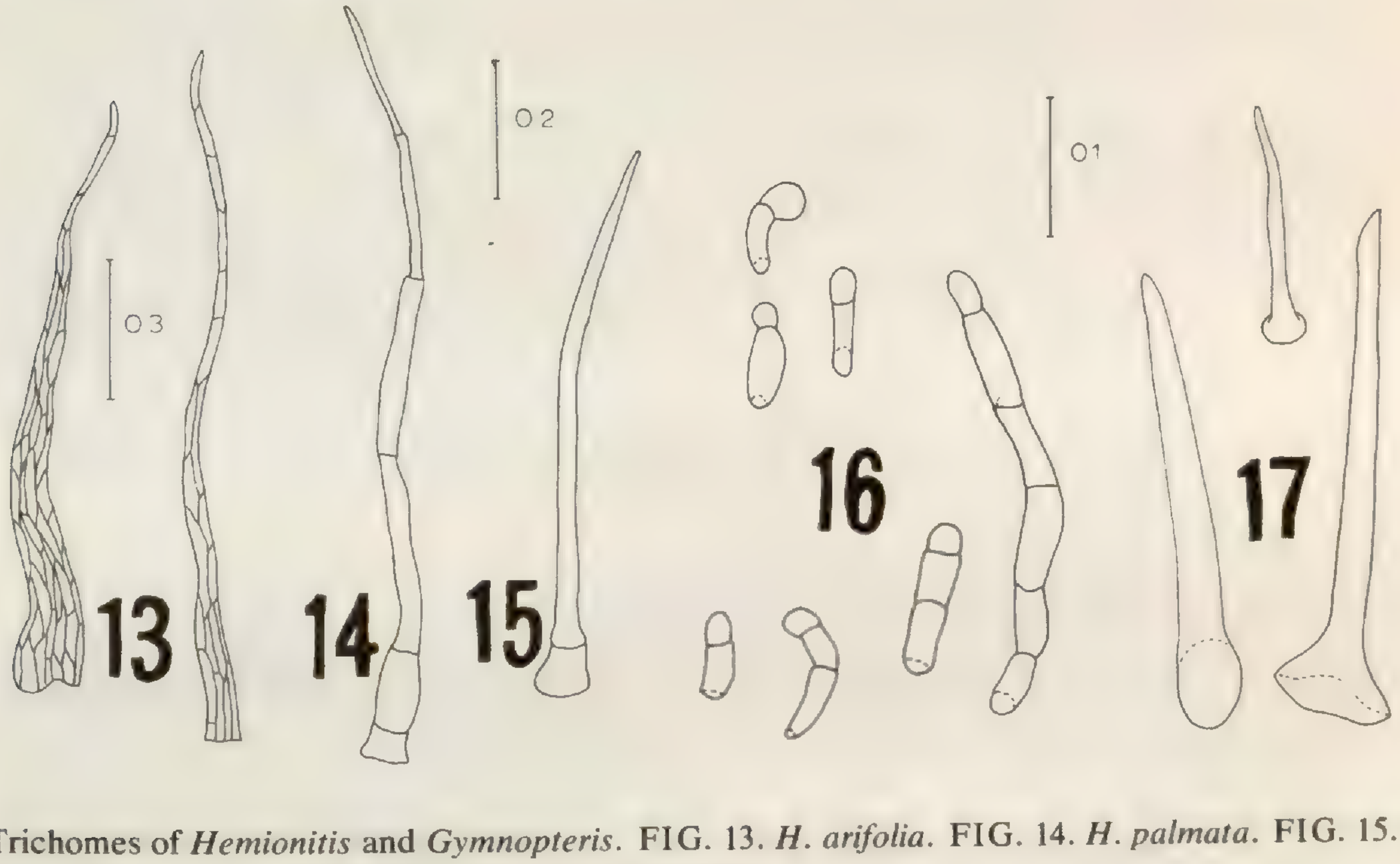
*The New York Botanical Garden, Bronx, NY 10458.

[1]Supported by a grant from the National Science Foundation. The drawings were made by Mrs. Julie Patterson.



Frond outlines of *Hemionitis* and *Gymnopteris*. FIG. 1. *G. bipinnata*. FIG. 2. *G. vestita*. FIG. 3. *G. subcordata*. FIG. 4. *H. pinnatifida*. FIG. 5. *H. elegans*. FIG. 6. *H. arifolia*. FIG. 7. *H. levyi*. FIG. 8. *G. tomentosa*. FIG. 9. *G. rufa*. FIG. 10. *H.* × *smithii*. FIG. 11. *H. palmata* × *pinnatifida*. FIG. 12. *H. palmata*.

Frond architecture.—Basically this character seems to keep the two genera, as commonly defined, apart. *Gymnopteris* has blades that are fully pinnate to bipinnate; those of *Hemionitis* are sagittate, palmate, or pinnatifid. *Hemionitis smithii (Fig. 10)* is pinnate with some pinnae broadly adnate and with the basal pinnae basiscopically auricled; it was postulated by Underwood (on the basis of an herbarium specimen) to be a hybrid between *H. palmata* and *Gymnopteris rufa*. This hypothesis is supported by gross and spore morphology.



Trichomes of *Hemionitis* and *Gymnopteris*. FIG. 13. *H. arifolia*. FIG. 14. *H. palmata*. FIG. 15. *H. levyi*. FIG. 16. *G. subcordata*. FIG. 17. *H. elegans*.

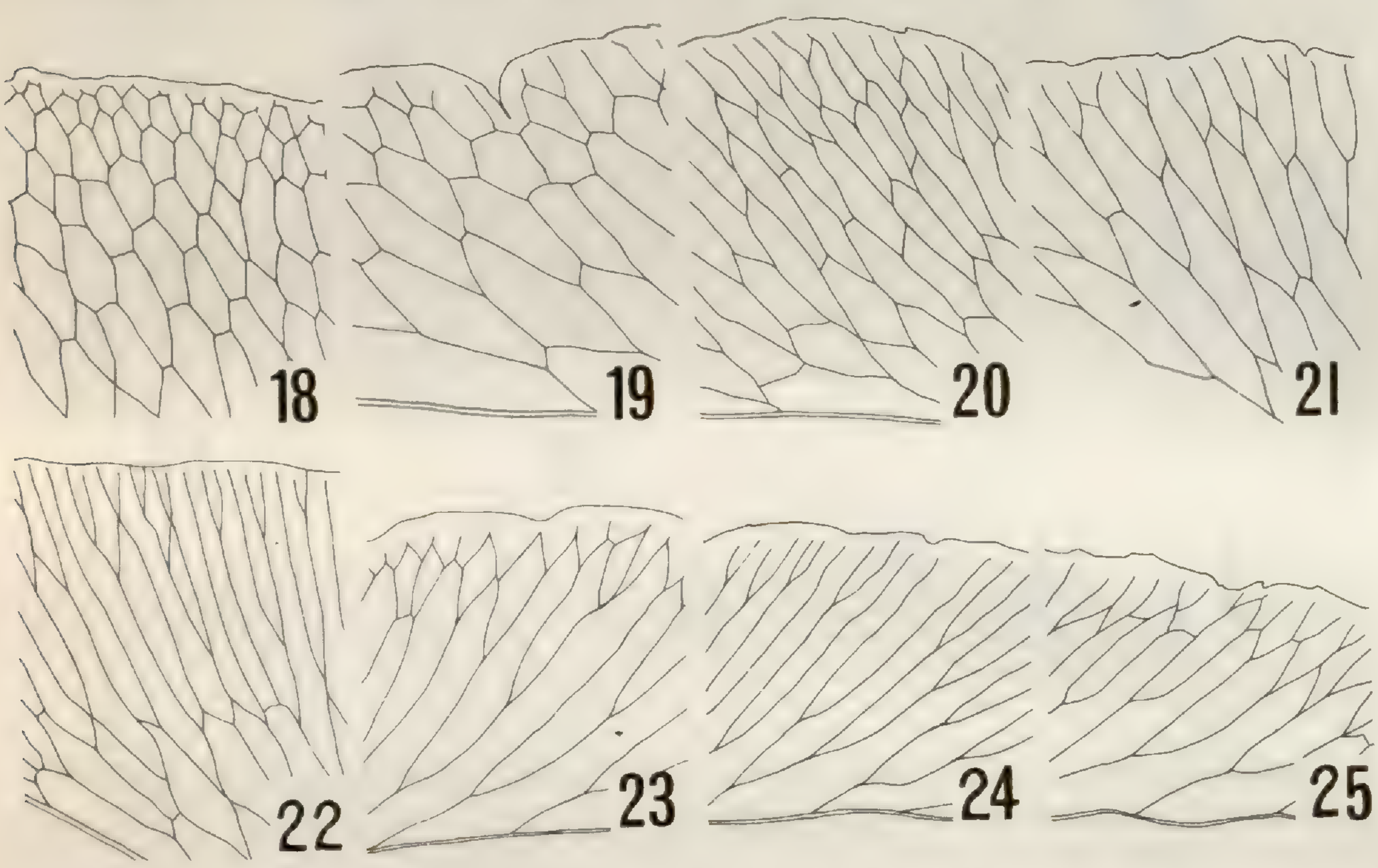
Geographic range.—Both *Gymnopteris* and *Hemionitis* contain species in both the New and Old Worlds, but no characters were found to correlate with geographic range. The Old World *H. arifolia* is quite distinct within *Hemonitis sensu stricto* in the characters mentioned above. Other than the spore ridges, these characters are not shared by the Asian species of *Gymnopteris*.

Indument.—In both genera the rhizome has scales and the blade is clothed with hairs. The hairs are generally more than one cell broad in *H. arifolia (Fig. 13)*, making them technically scales, although this point is generally not cited in the literature. Copeland (1947, p. 73) states that all *Hemionitis* species have laminar hairs, but the scales are illustrated in Hooker (1842, t. 74B). This transition from hairs to scales, often on the same frond, can also be seen in *Mohria*, and no great significance should be attached to it.

In most species of both genera the hairs are several cells long *(Fig. 14)*. Those of *H. elegans* are mostly very short, only one cell long, and sharp-pointed *(Fig. 17)*; those of *H. levyi (Fig. 15)* are also pointed, but often are two or three cells long. *Hemionitis subcordata* is nearly glabrous, but has scattered, short, multicel-

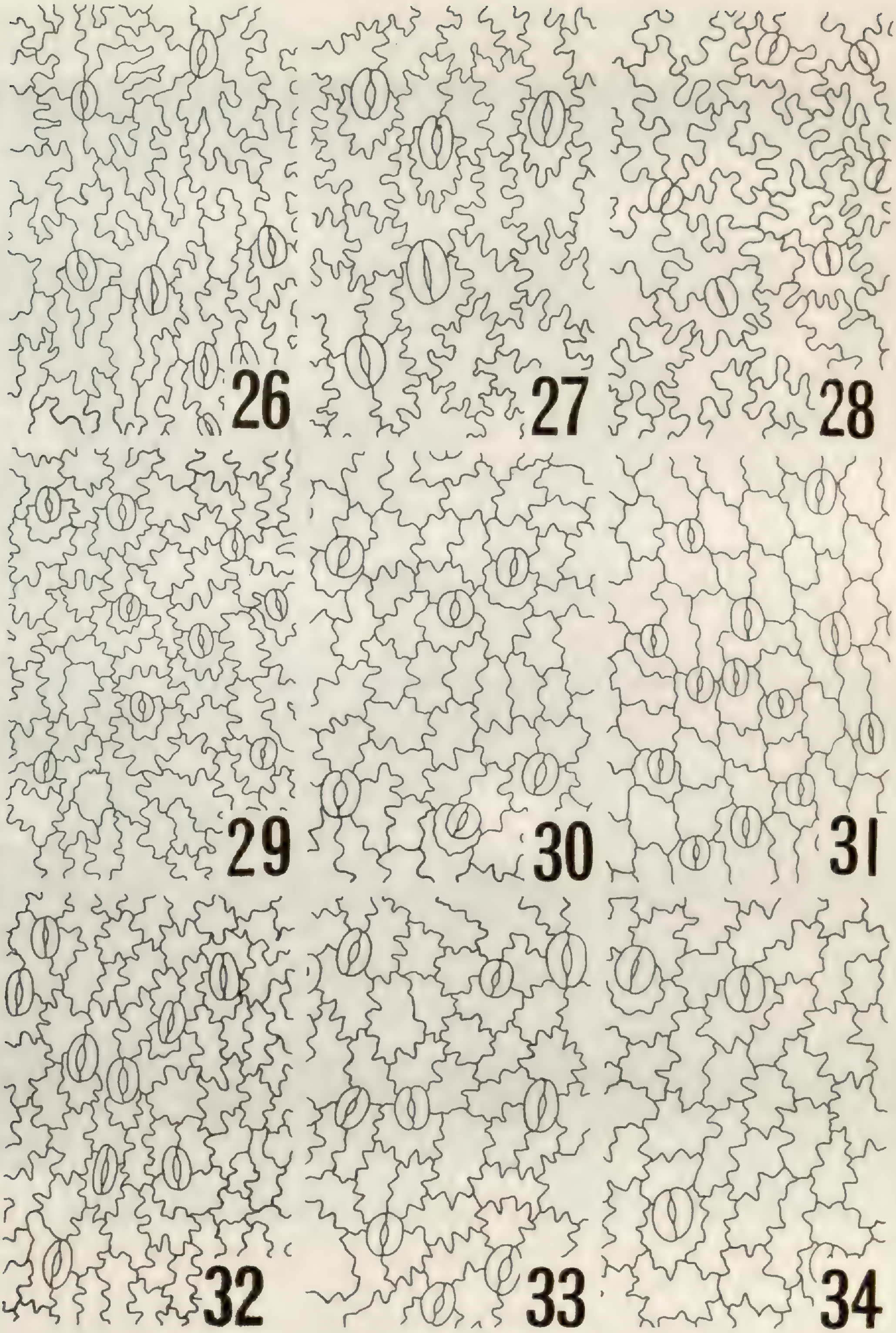
lular hairs whose cells are nearly equal in length *(Fig. 16)*, in contrast to the larger hairs of most species. These hairs have also been seen sparingly in *H. levyi* and *H. palmata* and are probably to be found as aberrant hairs in other species. These hair types can be seen with a hand lens.

Venation.—The distinction between net and free venation as a character to distinguish *Hemionitis* from *Gymnopteris* is not valid. Although some species of *Gymnopteris* do indeed have entirely free veins *(Fig. 24)*, and some species of *Hemionitis* have entirely net veins *(Fig. 18)*, this character does not hold consistently. Lellinger (1969) has pointed out that *G. subcordata* has largely net veins *(Fig. 22)*. There is a tendency for some species of *Hemionitis* to have rather extensive free veins near the margin *(Figs. 19–21)*. *Gymnopteris vestita* has mostly free veins with a few anastomoses near the margin *(Fig. 25)*. *Hemionitis* × *smithii*, the hybrid between *H. palmata* (net veins) and *G. rufa* (free veins), is largely free-veined near the midvein and netted near the margin *(Fig. 23)*.

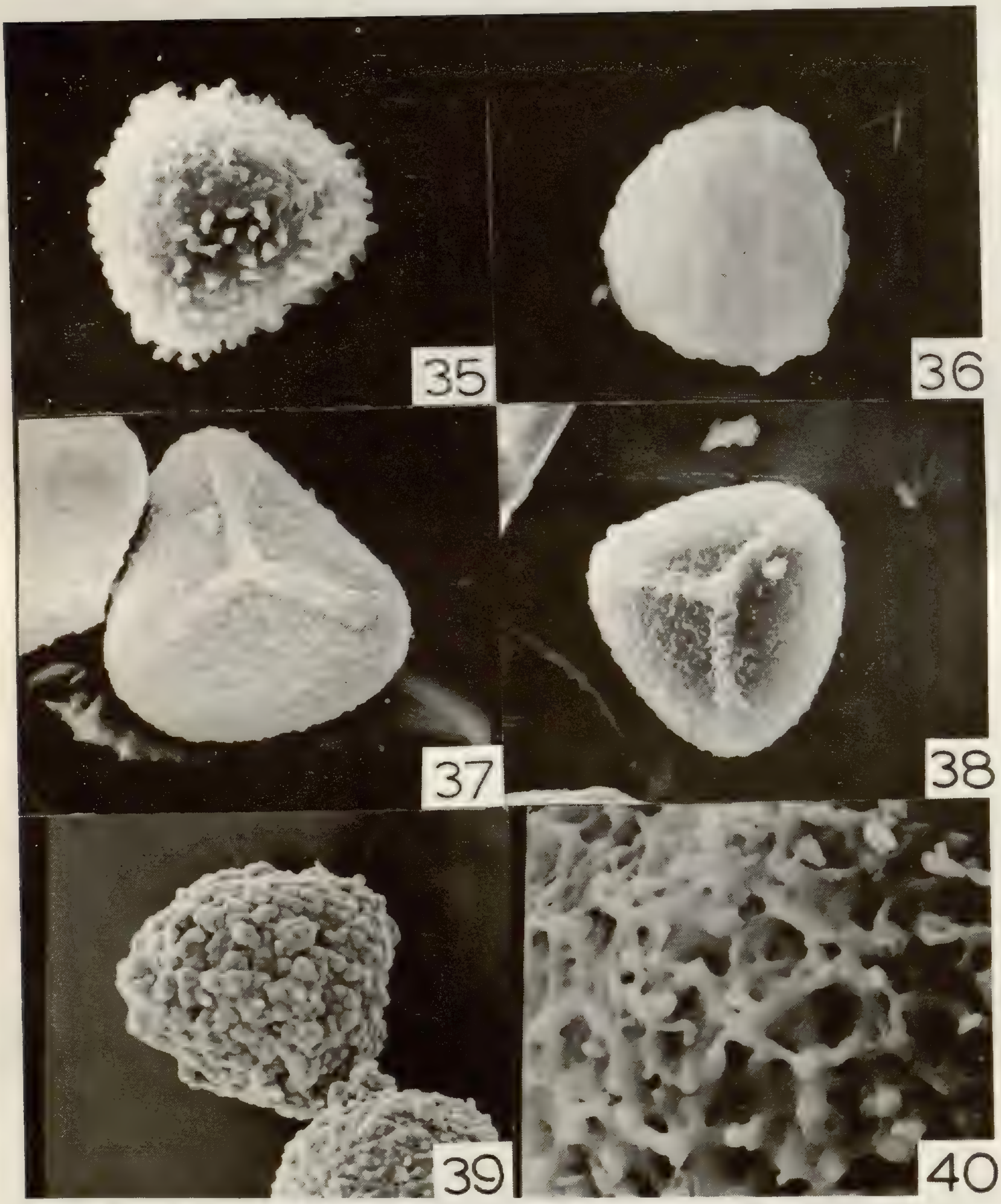


Venation patterns of *Hemionitis* and *Gymnopteris*, FIG. 18. *H. arifolia*. FIG. 19. *H. palmata*. FIG. 20. *H. elegans*. FIG. 21. *H. levyi*. FIG. 22. *G. subcordata*. FIG. 23. *H.* × *smithii*. FIG. 24. *G. tomentosa*. FIG. 25. *G. vestita*.

Epidermal pattern.—Leaf clearings showed some variation in epidermal patterns. Although there are no sharp distinctions between the species of *Gymnopteris* and *Hemionitis*, the patterns do seem to fall into two rough categories. *Hemionitis elegans (Fig. 26)*, *H. arifolia (Fig. 27)*, and *G. vestita (Fig. 28)* have highly contorted epidermal cells, whereas *H. palmata (Fig. 30)*, *G. subcordata (Fig. 31)*, *H. levyi (Fig. 33)*, and *H. pinnatifida* × *palmata (Fig. 34)* have more blocky cells. *Gymnopteris vestita* and *G. tomentosa* are somewhat



Patterns of the lower epidermis of *Hemionitis* and *Gymnopteris*, FIG. 26. *H. elegans*. FIG. 27. ***H.*** *arifolia*. FIG. 28. *G. vestita*. FIG. 29. *G. tomentosa*. FIG. 30. *H. palmata*. FIG. 31. *G. subcordata*. FIG. 32. *G. rufa*. FIG. 33. *H. levyi*. FIG. 34. *H. palmata* × *pinnatifida*.



Spores of *Hemionitis* and *Gymnopteris*. FIG. 35. *H. palmata*, distal view, × 1200. FIG. 36. *G. rufa*, distal view, × 1200. FIG. 37. *H. levyi*, proximal view, × 1200. FIG. 38. *H. pinnatifida*, proximal view, × 1200. FIG. 39. *H. palmata* × *pinnatifida*, distal view, × 1200. FIG. 40. *H.* × *smithii*, distal view, × 3000.

intermediate. Except for *G. subcordata,* these groupings generally agree with those based on chemical and spore evidence.

Chromosome number.—Chromosome counts have been reported for only three of the ten species: *Gymnopteris rufa, n* = 30 (Manton, 1958; Walker, 1966), *H. palmata, n* = 30 (Manton & Sledge, 1954; Wagner, 1963; Walker, 1966), and *H. arifolia*, *n* = 90, 2*n* = 90 (Abraham, Ninan & Mathew, 1962), *n* = 120, 2*n* = 120 (Manton & Sledge, 1954). Both reports for *H. arifolia* are for apogamous polyploids. A study of stomate and spore sizes was made to determine whether other species might possibly be polyploids. The results are not conclusive. In both stomate length and spore diameter *H. arifolia* is among the largest. Other species, however, are inconsistent. *Gymnopteris rufa,* a known diploid, has long stomates but small spores. *Gymnopteris vestita* and *G. bipinnata* have the largest spores but only medium-sized stomates. The hybrid *H. palmata* × *pinnatifida* has large stomates but small spores. Thus, there is no apparent basis for extrapolating probable ploidy levels at this time.

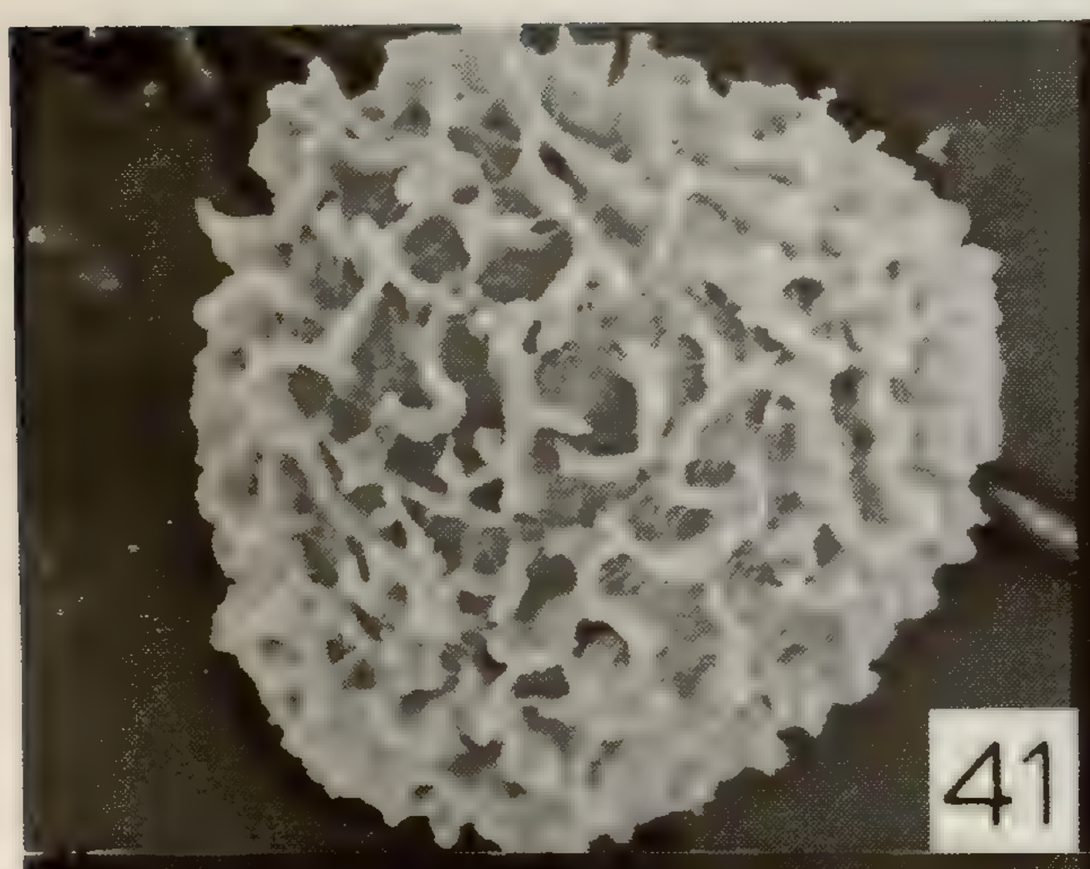
TABLE 1. STOMATE AND SPORE SIZES IN *HEMIONITIS* AND *GYMNOPTERIS*[1]

	Stomate length in μm	*Spore diameter in μm*
H. arifolia	62.5	44.5
G. bipinnata	36.8	54.1
H. elegans	47.6	37.3
H. levyi	48.1	36.7
H. palmata	45.5	32.0
H. palmata × pinnatifida	61.6	36.4
H. pinnatifida	48.3	37.1
G. rufa	55.5	31.7
H. × smithii	51.5	34.8
G. subcordata	47.6	31.8
G. tomentosa	38.2	32.6
G. vestita	43.1	57.0

[1]Figures represent averages of 20 measurements of representative specimens.

Chemical evidence.—Dr. David Giannasi, in a study of the phenolic compounds in the species of *Hemionitis* and *Gymnopteris* (1974), has shown that according to their compounds, the species fall into two distinct groups that cut across traditional generic boundaries. Each group has several distinct compounds not found in the other. One group, including *H. pinnatifida, H. levyi, H. palmata,* and *G. rufa,* has flavones and methylated flavonols, whereas the other species, *H. elegans, H. arifolia, G. subcordata, G. tomentosa, G. vestita,* and *G. bipinnata,* contain regular flavonols. These groupings match exactly those based on spore morphology.

Spores.—Within *Hemionitis* and *Gymnopteris* nearly all the species can be distinguished on the basis of their spore morphology, but they generally fall into two major groups: those with low to high tubercles *(Figs. 35–40)* and those with ridges *(Figs. 41–46).* Of the tuberculate species, *H. palmata (Fig. 35)* stands out with the longest projections. Spores of *H. pinnatifida (Fig. 37), H. levyi,* and *G. rufa* are very much alike with broad, low bumps. Among the species with ridges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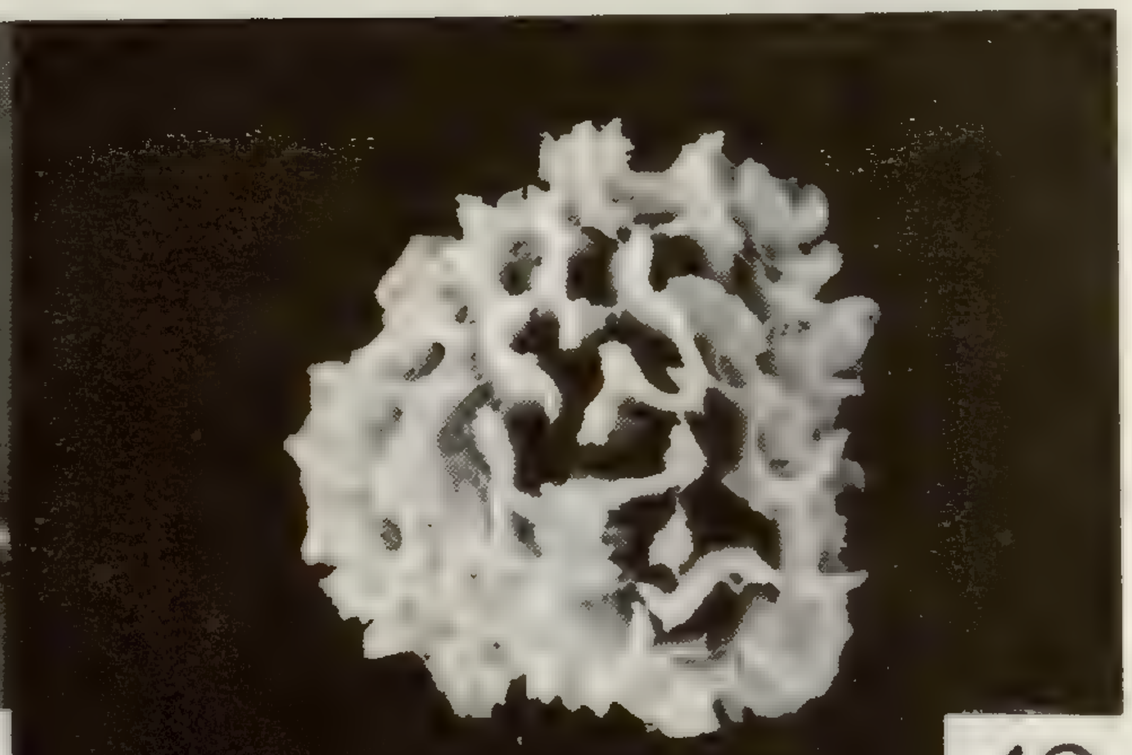
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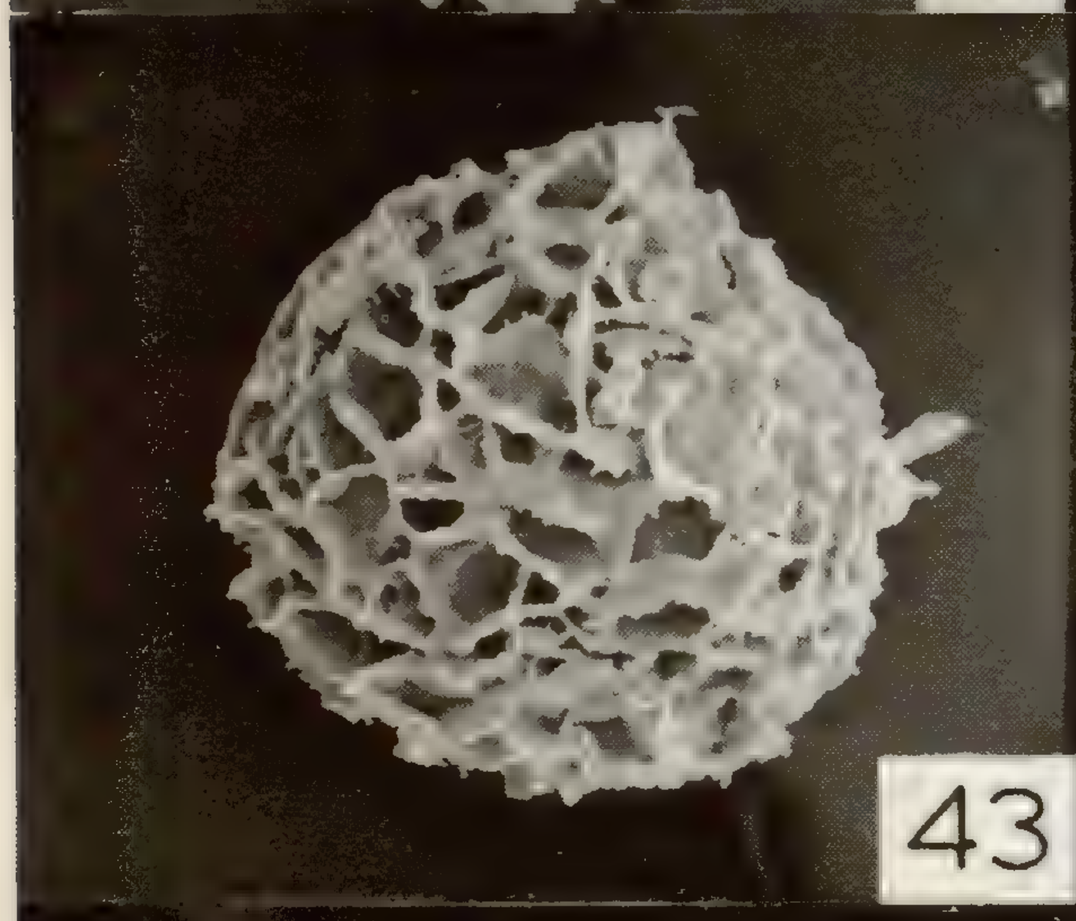
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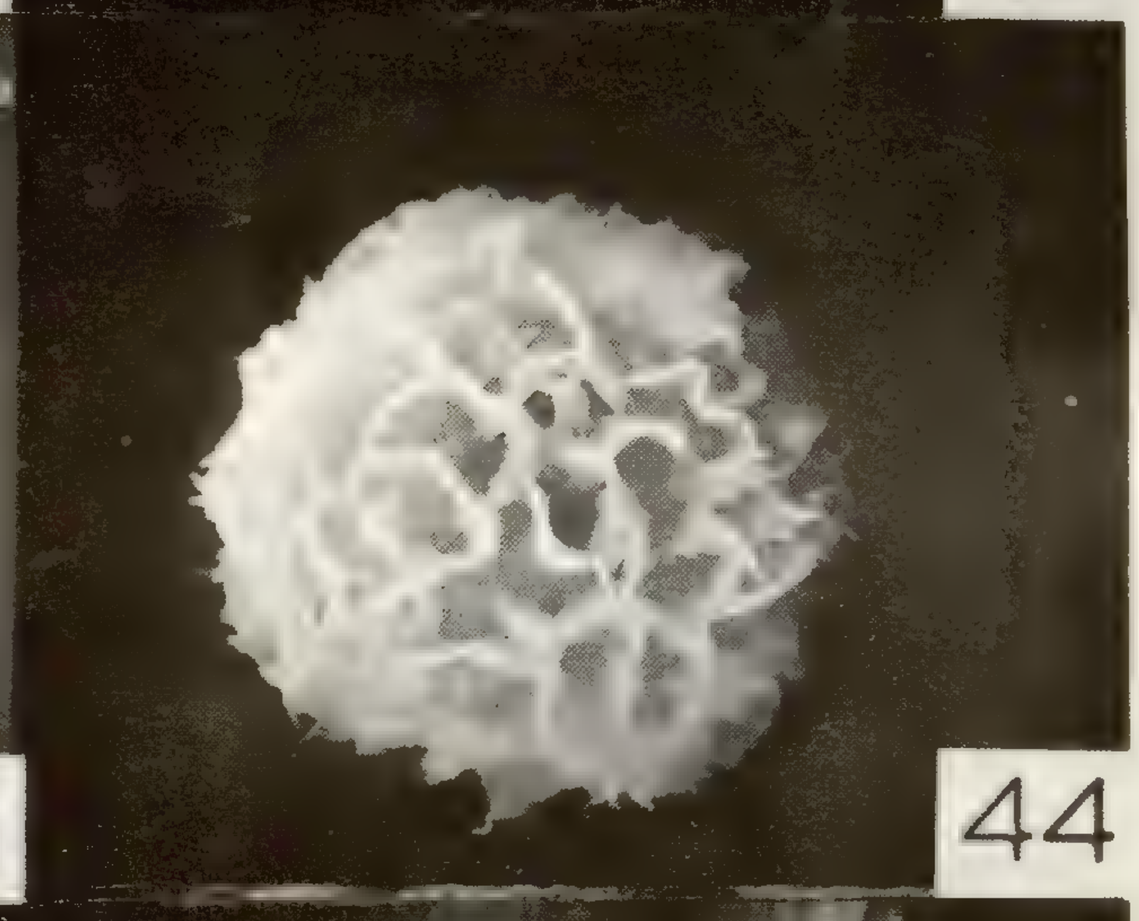
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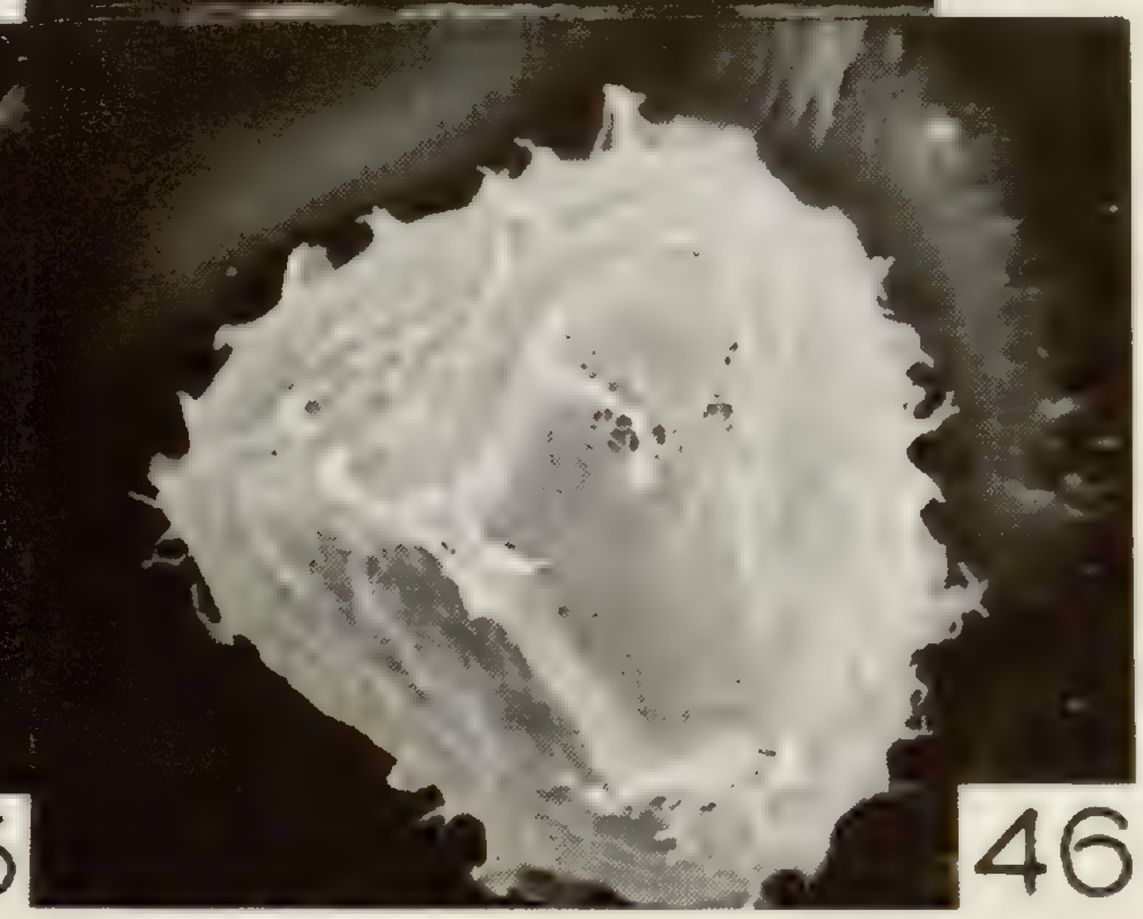
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Spores of *Hemionitis* and *Gymnopteris*. FIG. 41. *H. arifolia*, distal view, × 1200. FIG. 42. *G. tomentosa*, distal view, × 1200. FIG. 43. *G. bipinnata*, distal view, × 900. FIG. 44. *G. vestita*, distal view, × 900. FIG. 45. *G. subcordata*, proximal view, × 1200. FIG. 46. *H. elegans*, proximal view, × 1200.

on the spores, *G. subcordata (Fig. 45)* has the most slender and highest ridges. *Hemionitis elegans (Fig. 46)* has the least developed ridges and has peculiar, small caverns and small, slender projections about them. *Gymnopteris bipinnata* and *G. vestita* have numerous, fine, fingerlike projections on the ridges.

It is interesting to note that the two hybrids known in the genus both occur between species with tuberculate spores: *H. palmata* × *pinnatifida (Fig. 39)* and *H. palmata* × *rufa*. The hybrids show some abortion and some large, round spores with tubercles of length intermediate between those of the parents.

CONCLUSIONS

From these data we can see the generic boundaries between *Hemionitis* and *Gymnopteris* as traditionally held are not tenable. Leaf architecture is the only character separating the two. On the other hand, at least two lines of evidence point to two groups of species that cross the generic lines. Results from phenolic chemistry and spore morphology agree perfectly and epidermal patterns fall into roughly the same groupings, those with crested spores and regular flavanols generally having the most contorted epidermal patterns. Without any gross morphological differences, however, it does not seem reasonable to give these groups generic rank.

The relationship of *Hemionitis* to other genera is not entirely clear. *Hemionitis* in the strict sense was placed by Copeland (1947) closest to *Bommeria* (rather than *Gymnopteris* even). Lellinger (1965) also placed it closest to *Bommeria* and not far from Gymnopteris and *Paraceterach*. The spores of *Bommeria* are quite different from those of *Hemionitis*. Those of the former are nearly smooth with only slight bumps on the surface, somewhat like those of certain species of *Notholaena*. On the other hand, the spores of *Trachypteris,* which bears little superficial resemblance to *Hemionitis,* are nearly identical to the crested-spored species of *Hemionitis*. This is particularly surprising on the basis of its having its blade densely covered with broad, toothed scales, quite unlike anything found in *Hemionitis*. Further study and re-evaluation of a broad array of characters in *Trachypteris, Saffordia, Paraceterach, Bommeria,* and perhaps other genera are needed.

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Axenic Culture of the Aquatic Fern, Salvinia[1]

ALLEN V. SEILHEIMER*

Salvinia has potential as an experimental organism because of its small size, simplicity, and rapid growth. A limited amount of work has been done on reproduction and growth of *Salvinia*. Cultural studies employing nonsterile conditions have revealed information on vegetative growth (Rajan, Betteridge & Blackman, 1971), photoperiodic responses (Nakayama, 1952), and competitive growth (Chatworthy & Harper, 1962). The effect of growth regulators (Gaudet & Huang, 1967; Gaudet & Koh, 1968) and growth in a simulated natural environment (Gaudet, 1973) have been studied using aseptic culture. It is the intent of this note to report a simple, reproducible method by which *Salvinia* can be surface-sterilized and cultured aseptically.

FIG. 1. Sterile stock culture of *Salvinia natans* in test tube and *Salvinia auriculata* in 125 ml Erlenmeyer flask (left) on Hutner's medium solidified with agar. Erlenmeyer flask (right) shows crowded pure culture of *S. auriculata* on liquid Hutner's medium.

The nonwetting property of the floating leaves makes sterilization of *Salvinia* difficult. Gaudet and Koh (1968) have reported a method of surface sterilizing *Salvinia* which I found difficult to reproduce. Their method was not described in sufficient detail to be reproduced and proved unreliable. The method reported here is similar to that used for surface sterilizing *Lemna* (Hillman, 1961). Plants consisting of the two youngest floating leaves, one submerged leaf, and a submerged shoot apex, which are relatively free of debris and other organisms, are

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selected under a dissecting microscope and washed three times in sterile tap water in a 250 ml Erlenmeyer flask by shaking with a test tube shaker (Super-mixer, Matheson Scientific Co., Chicago) for about one minute. Then they are shaken in a sterile aqueous solution of Tween 80 (10^{-5}, v/v) to break the surface tension of resistant fungal and bacterial spores. The plants are left in sterile tap water for 24 hours to allow resistant spores to germinate. Then they are immersed in 0.2% bleach (a 1 to 26 dilution of 5.25% commercial sodium hypochlorite bleach) until the leaves begin to turn white (ca 2–5 min). Bleach obtained at different times may be of different strengths; therefore, some trial bleaching of fronds is necessary to determine the proper length of time in the bleach. The first plants removed should be bleached only slightly, whereas the last plants removed should be bleached completely white. The bleach is removed by two rinses in sterile tap water and three rinses in sterile distilled water with brief shaking. The plants are placed singly in 60 × 15 mm plastic Petri plates containing sterile Hutner's growth medium with 1% sucrose (Hutner, 1953). Cultures placed in continuous fluorescent light (ca 300 ft-c) at about 30°C should show growth of *Salvinia* and the presence of contaminates (if any) within one week. After sterile plants have been obtained, they grow well in 125 ml Erlenmeyer flasks with 50 ml of Hutner's growth medium. In reduced continuous light (125 ft-c) and temperature (about 22°C) stock cultures can be maintained on growth media solidified with 1% agar for 6 months or longer (*Fig. 1*). *Salvinia natans* and *S. auriculata* have been obtained successfully in pure culture using this technique.

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Two New Polystichums From the Himalayas[1]

N. C. NAIR*

During a study of *Polystichum* specimens from India and adjoining countries in the herbarium of the Komarov Botanical Institute, Leningrad, U. S. S. R., I discovered two new taxa which are described below. Both of them were filed under the name *P. aculeatum,* and the labels on most of the herbarium sheets indicated that they were identified as *P. aculeatum* by C. Christensen for his "Index Filicum." That the new taxa are distinct from *P. aculeatum,* a species found in the Indian subcontinent and certain parts of Asia, as well as in Europe, is clear from an examination of a photograph of the type of *Polypodium aculeatum* L. (Hort. Leiden, *Van Royen*), which was obtained from the Rijksherbarium in Leiden. (For a discussion of the typification of this species see Alston, A. H. G. 1940. J. Bot. Brit. & For. **78**: 160–164).

Polystichum longipinnulum N. C. Nair, sp. nov. Fig. 1.

Polysticho setifero (Forsk.) Moore ex Woynar affine, sed differt stipitibus dissiti-squamatis et pinnulis lineari-lanceolatis vel lineari-lanci-subfalcatis, latere acroscopico basibus valde manifeste auriculatis latere basiscopico serraturis spinulosis, pinnulis inferioribus penitus lobatis, interdum pinnatifidis.

Rhizome unknown. Stipes up to 25 cm long, pale, grooved on the upper side, bearing several scattered, large, lanceate, shining, purplish-brown, hyaline-margined scales 13–14 mm long, 2–4mm broad at the base, and smaller, fibrillose, brown scales throughout the stipe, rachis, and pinna midribs. Lamina triangular, up to 60 cm long, 32–34 cm wide, bipinnate, the basal (or rarely the subbasal) pinnae the largest, the upper pinnae very gradually reduced. Pinnae alternate, up to 18 cm long, 1.4–3.5 cm wide at the base, subsessile or sessile, closely pinnate throughout; pinnules opposite or alternate, subsessile or shortly stalked, not decurrent, linear-lanceolate or linear-lanceolate-subfalcate, 15–22 mm long, 3–4 mm wide, acute at the base, with a prominent, auricled acroscopic base and the basiscopic base narrowed to the midrib, the margins spinulose on the basiscopic side, those in the lower pinnules deeply lobed and the pinnules thus pinnatifid, the lobes aristate, the veins of each lobe with the acroscopic branch ending in a sorus and the basiscopic branch 1-forked with the lower branch entering the arista; lower surface of the lamina very sparsely scaly or glabrous; upper surface glabrous when old. Sori 7–10 pairs per pinnule, 1–2 pairs on the auricled lobe, the others in 1 row on each side of the midrib and rather nearer to it than the pinnule margins. Indusium very small, brown, peltate, not covering the sorus at maturity, often deciduous.

TYPE: Nepal, *Wallich* in ca 1885 (LE, Nair photo 3, CAL).

PARATYPES: Iserra (Khassia), India, 1440 m, 28 Sept 1867, *C. B. Clarke 5114* (LE). Darjeeling, India, 2250 m, 17 Aug 1885, *C. B. Clarke 27021 D* (CAL, LE).

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[1] The author is thankful to the authorities of the Komarov Botanical Institute, where this work was completed under the Indo-Soviet Cultural and Scientific Exchange Programme. He is also grateful to Dr. A. Bobrov, of the Institute, for very useful discussions and for help with the photography, to Dr. N. C. Majumdar, Botanical Survey of India, for the Latin descriptions, and to Dr. K. Subramanyam, former Director of the Botanical Survey of India, for his interest in the work.

Fig. 1. Holotype of *Polystichum longipinnulum*. Fig. 2. Holotype of *Polystichum setiferum* var. *crenatum*.

Polystichum setiferum var. crenatum N. C. Nair, var. nov. Fig. 2

Differt a *P. setifero* var. *setifero* pinnulis usque ad 16(18) mm longis, 4 mm latis ad punctum latissimum, nitidis, subcoriaceis, latere proximali recto et apicem versus dentato, latere distali leviter crenato, apice plus minusve rotundato aristato, loborum apicibus latere distali non aristatis.

TYPE: Punjab, India, *King* in 1878 (LE, Nair photo 4, CAL).

PARATYPE: Punjab, *King* (LE).

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A Peculiar New Species of Trichomanes sect. Selenodesmium and Several of its Probable Hybrids[1]

DAVID W. BIERHORST*

On December 27, 1965 a peculiar species of *Trichomanes,* first thought to be in the sect. *Davalliopsis,* was collected in New Caledonia. It proved to be the first species of *Trichomanes* sect. *Selenodesmium* that has leaf blades more than one cell thick. The relatively exposed habitat (altitude ca. 300 m along the trail from the Dumbea Dam to Montagne des Sources) which, however, seemed to be supplied with subsurface water, correlates with the nearly sclerophyllous fronds of the new species. Substratum samples unfortunately yielded no hymenophyllaceous gametophytes, only thallose ones identified as *Blechnum* sp. and filamentous ones clearly belonging to *Schizaea fistulosa. Bierhorst NC460* included two mature specimens, and *Bierhorst NC465* included one sterile, half-grown plant with associated substratum. The material was preserved in a chromic acid-acetic acid-formaldehyde solution in the field and was later transferred to glycerine alcohol. Type material will be dried and deposited in the Gray Herbarium, Harvard University.

Freehand sections of all parts of the plant were prepared and stained with 1% Methyl Green for 5 min followed by two rinses in water. The sections illustrated in *Figs. 11* and *13–18* were prepared in this manner. The cleared leaf shown in *Figs. 4* and *20–22* was bleached in "Clorox" until white (ca. 15 min; monostromaticous species generally take 1-3 min), rinsed with three changes of water, dehydrated in 70%, 95%, and 100% ethanol (5 min each). It was then stained with Fast Green (1% in 100% ethanol) for 3–5 min, rinsed in two changes of 100% ethanol (total ca. 5 min), then one change of 1:1 xylene-absolute ethanol, then cleared in xylene (two changes of 5 min each), and finally mounted in synthetic resin "HSR." The new species is designated:

Trichomanes polystromaticum Bierhorst, sp. nov.

Planta terrestris. Rhizoma crassum adscendens, trichomata numerosa fuscata attenuata articulata plerumque 2 mm longa ferens. Stipites tenaces fasciculati asperi fuscati, trichomata decidua sparsim ferentes. Stipites penitus alati vestigialiter, ala decidua basi. Lamina bipinnata, segmentis ultimis incisis, stratis 2 vel 3 cellularum composita, coriacea, cellularum parietibus crassis conspicue reticulatis. Pinnae anadromicae. Rachis juvenis omnino alata trichomata ferens. Nervatio aperta sed paucis venis liberis distaliter convergentibus. Radices stipitis lateribus singulatim basaliter enatae. Sorus terminalis in lobo basali vel subbasali in pinnulae latere acroscopico. Involucrum campanulatum, ore integrum constrictum, basi contractum, plerumque 0.8 mm × 1 mm. Receptaculum longe exsertum.

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Sporangia numerosa, plerumque 200 μm lata, 32 sporas triletas foveatas plerumque 21 × 36 μm capientia. Annuli cellulae 12–14.

TYPE: Along trail from Dumbea Dam to Montagne des Sources, ca 300 m alt, New Caledonia, *Bierhorst NC460* (to be deposited at GH).

OBSERVATIONS AND DISCUSSION

The most conspicuous feature of *Trichomanes polystromaticum* is its several-layered lamina (*Fig. 11*), to which the specific epithet refers. This is reflected in the appearance and texture of the frond, which approaches sclerophyllous. Among other described species of the family, *Trichomanes (Cardiomanes) reniforme* of New Zealand, *T. (Davalliopsis) elegans* of tropical America, and several species of *Hymenophyllum* subg. *Mecodium* sect. *Diplophyllum* share this feature (see Morton, 1968). The relationship between sect. *Selenodesmium,* to which *T. polystromaticum* belongs along with some ten other species, some of which are poorly defined, and the monotypic sect. *Davalliopsis* was suggested by Copeland (1938). He, however, emphasized distinctiveness of epidermal wall structure to the point of further suggesting also that the resemblance (in habit and frond and soral form) might be superficial. His first suggestion now seems more plausible.

Despite the fact that *Trichomanes polystromaticum* has a multilayered leaf, like other polystromaticous species of Hymenophyllaceae it bears no stomata nor any significant intercellular spaces within the lamina. In fact, no stomata have ever been reported in this family. This, in addition to the fact that several of the other multilayered species exhibit only the unilayered condition on young plants, has been interpreted (Holloway, 1923) to indicate that the extant polystromaticous species were derived from monostromaticous ones. Other morphological evidence (Copeland, 1938; Bierhorst, 1974) strongly indicates that among extant Hymenophyllaceae, small creeping species, all of which are monostromaticous, present the most primitive morphology.

The marginal initials in the growing leaf of *T. polystromaticum* divide by means of new walls formed at right angles to the plane of the lamina. This agrees with all other described hymenophyllaceous marginal meristems, including those of polystromaticous species, but differs sharply from all those described from other fern families (see Bower, 1923).

The position of the sorus varies on the pinnules. In the distal 2/3 of the frond, all are inserted on the lowest segment (*Fig. 7*). In the proximal 1/3 of the frond, the sori are on the second (*Fig. 5*) or third (*Fig. 6*) acroscopic segment. The lowest acroscopic segment when sterile is often represented by a near-extinct lobe.

The involucre is elliptical in cross-section and has two lateral veins, as is general for the Hymenophyllaceae. Except for the end between the two veins and distal to the level where the constriction begins, the involucre, too, is composed of several cell layers (center of the distal part of the involucre, *Fig. 8*). The mouth of the involucre is elliptical with angular edges. The receptacle with its collection of sporangia tends to force it into a circular outline (*Fig. 6*), but when sporangia fall away, the opening reassumes its original, bilateral form.

Holotype of *Trichomanes polystromaticum*. FIG. 1. Holotype plant. FIG. 2. A pinna. FIG. 3. Sori. FIG. 4. A cleared ultimate segment.

The receptacle is long-exserted and typical for its type. After the sporangia are produced in their characteristically basipetal-gradate sequence, no extended, sterile portion of the receptacle is produced. The absence of this feature, which is one of the major features of the Hymenophyllopsidaceae, makes it futile to compare *T. polystromaticum* with that family, despite some similarity in leaf structure.

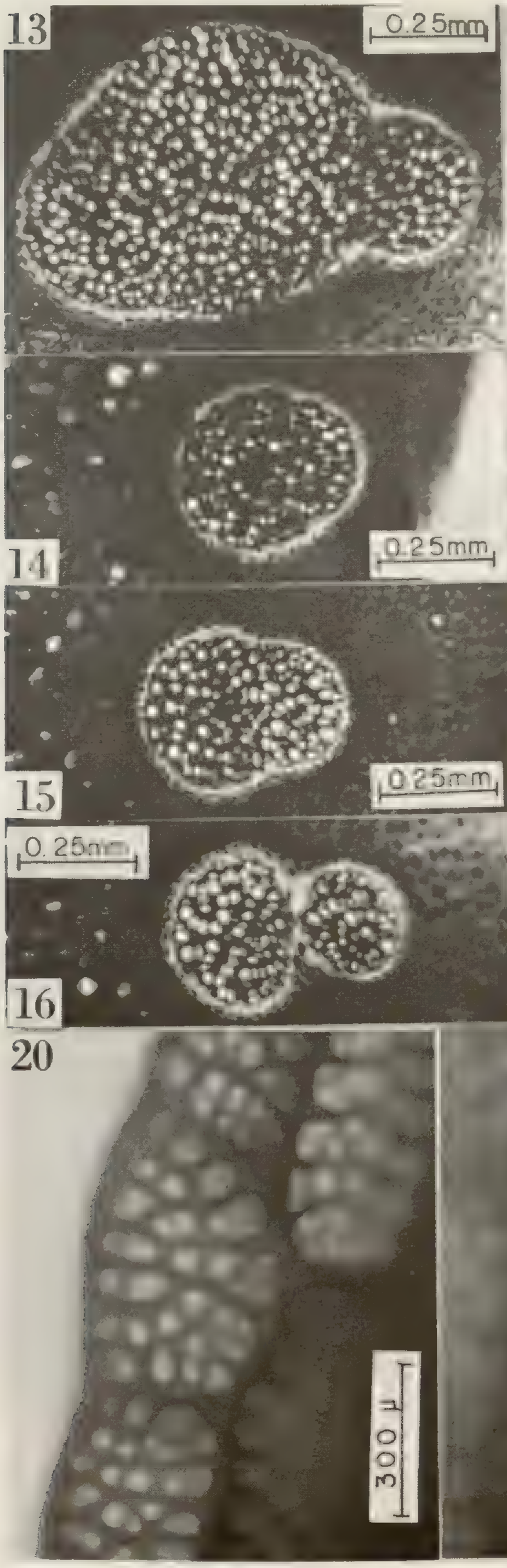
Sporangium size, spore number per sporangium, high sporangium number per receptacle, and gametophytes one-celled when shed all appear relatively uniform among species of *Trichomanes* considered to be in sect. *Selenodesmium*. The new species is no exception. Preserved material of five other species collected by the author in Fiji, New Caledonia, and New Guinea, as well as dried herbarium material in the Gray Herbarium were available for comparison.

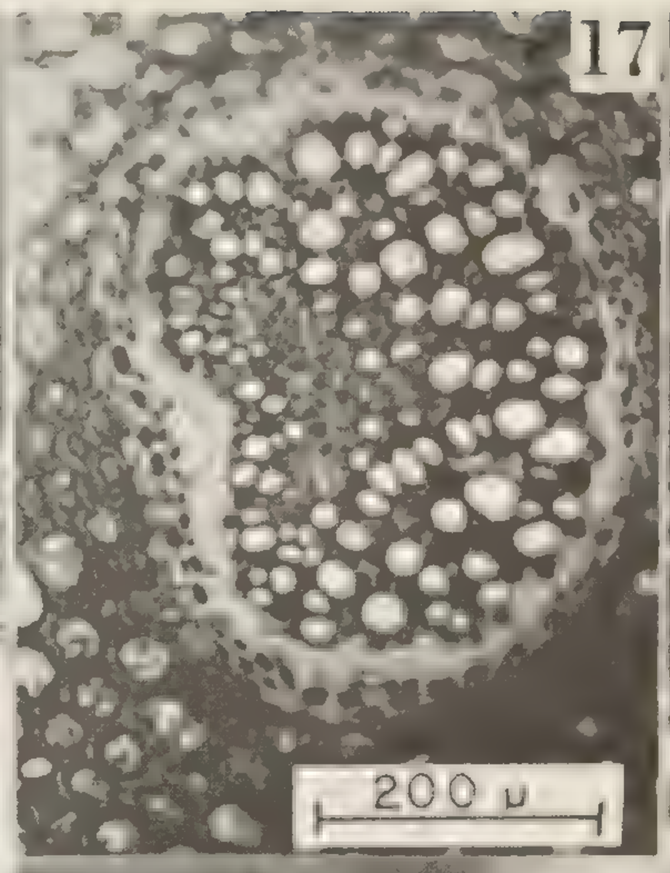
Patterns of outer epidermal wall thickening (*Figs. 20–22*), especially of the marginal cells, are reasonably diagnostic in sect. *Selenodesmium*. The manner in which the material is prepared, however, seems critical. The cells illustrated in *Figs. 20–22* were stained with an acid stain. When material was unstained or stained with a basic stain such as Safranin or Methyl Green, areas of the wall which are not significantly thicker than elsewhere do not show up, and hence the fainter bars of the reticulum are not visible. The more or less rounded areas within this wall pattern have generally been termed "pits." This has led to no misconceptions insofar as the author is aware, but anatomically the term is applied in error. There are no areas of the outer wall where secondary layers are absent. The continuous secondary wall is peculiarly differentially deposited to yield a reticulate or pseudo-pitted appearance.

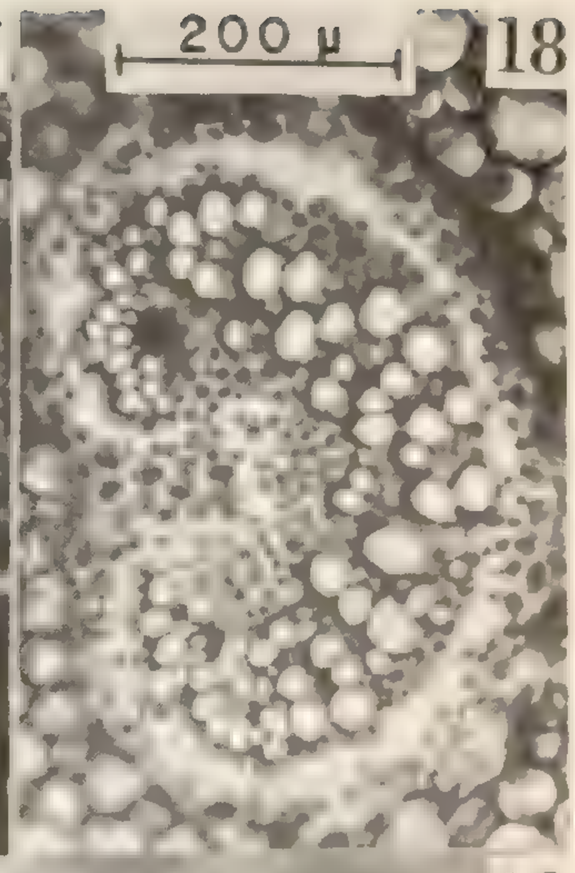
Occasional convergent vein tips (e.g., the upper two in *Fig. 4*) are interesting, but seem quite unrelated to areole origin in fern leaves with fully or partly anastomosing venation. Throughout the Hymenophyllaceae, as well as in most other ferns with dichotomous venation, marginal initials of the lamina produce distinct files of cells in which cellular differentiation and maturation progresses toward the margin (see figures of Goebel, 1930; Hagemann, 1965). Within the marginal meristem certain cells are initials of the procambium and others are not. The lamina shown in *Fig. 4* was in no way different. The convergence was due to the failure of cells within three cell lineages to enlarge near the distal ends of the two veins on either side, but the three files of cells were in no other way disturbed.

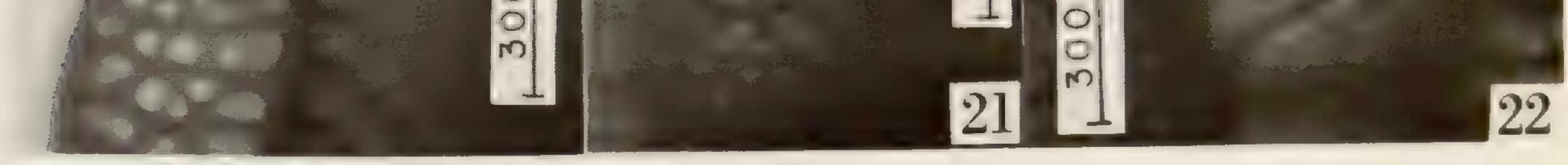
The stem anatomy of *T. polystromaticum* is consistent with that of all described *Trichomanes* species with upright, relatively robust stems. A highly parenchymatized ("vitalized") central mass of xylem (*Fig. 13*) is present. Traces to the phyllophores (one is shown departing at the right in *Fig. 13*) arise in a pseudo-spiral, reflecting the attachment of the external organs. The pseudo-spiral is made up of subopposite pairs of phyllophores, with each successive pair rotated nearly 180° from the pair above or below. This type of attachment in *Trichomanes* grades into a true spiral when the sub-paired arrangement is lost and into a distichous arrangement in which the rotation of successive pairs is 0°. This latter condition is considered to represent the most primitive condition within the family and is found in groups of species with thin, creeping stems, like *Trichomanes* sect. *Gonocormus* and sect. *Crepidomanes* (Bierhorst, 1973, 1974).

Holotype of *Trichomanes polystromaticum*. FIGS. 5–7. A sorus on the second, one on the third, and one on the first (center of three) acropetal segment of a pinnule. FIG. 8. A single sorus. FIG. 9. Excised receptacle with sporangia. FIG. 10. The stem with petiole bases and roots. FIG. 11. Lamina cross-section. FIG. 12. A spore.









Holotype of *Trichomanes polystromaticum*. FIG. 13. The stem stele with departing phyllophore trace at right. FIG. 14. Phyllophore trace. FIGS. 15, 16. Phyllophore trace dividing to produce a leaf trace (left) and a pseudoaxillary bud trace (right). FIGS. 17, 18. The leaf trace ca 0.5 cm and ca 1.5 cm above the level of Fig. 16. FIG. 19. Stem trichomes. FIGS. 20–22. Outer lamina epidermal cell wall thickenings on a marginal cell, submarginal cell, and an intervenal cell, respectively.

TABLE I. SELECTED CHARACTERISTICS OF *Trichomanes dentatum*, *T. polystromaticum*, AND THEIR HYBRIDS.

Source	*Collector*	A[1]	B	C	D	E	F	F_c	G	H
				Trichomanes dentatum						
New Caled.	Franc 1407	3-3.5	1	5-9	–	–	25.5(25-26)	27		0
Fiji	Smith 6013	3-4	1	5-8	+	–	25(21.5-28)	26.5		0
Society Is.	de La Rue	3-4	1	5-9	+	–	26.5(25-31)	28		0
Fiji	Degener 14137	3-4	1	5-9	+	–	25(23-28)	26.5		0
Samoa	Reinecke 86b	1.5-2	1	5-9	+	–	25.5(25-28)	27		0
Fiji	Smith 1349	2.5-3.5	1	6-12	+	–	26(25-28)	27.5		0
Tahiti	Wilkes 22[2]	2.5-3.5	1	5-9	+	–	25.5(23-26)	27		0
New Caled.	Franc 366	2.5-3.5	1	6-8	–	–	25(21.5-26.5)	26.5		0
Cook Is.	Parks 22034	2-3	1	6-9	+	–	26.5(23-28)	28		0
Fiji	Bierhorst Fx1	3-4	1	5-9	+	–	27(23-29)	—		0
				Trichomanes dentatum × *polystromaticum*						
New Caled.	Vieillard 1663[2]	3-3.5	2-3	3-5	–	–	25.5(23-31)	27		0
New Caled.	McKee 4438	2.5-3	2	5-9	–	–	28.5(24-30)	30.5	29 × 22	23
New Caled.	Buchholz 1209	3-3.5	2	5-8	–	–	30(26-33)	32	32 × 22	37
New Hebr.	Morrison 20VII1896	2-3	1	5-9	+	–	29(28-30)	31	32 × 16.5	31
New Hebr.	Morrison 16VI1896	2.5-3.5	2	8-13	+	–	28(23-32)	30	30 × 21	61
				Trichomanes polystromaticum						
New Caled.	Bierhorst NC460	ca. 1	2-3	2-4	–	+	36(33-38)	—		0

[1] A = Involucre, L:W. B = Lamina thickness, number of cells. C = Maximum number of cells between free vein endings. D = Involucre mouth, apical flaring. E = Involucre, subapical constriction. F = Average diameter of tetrad spores in μm, the range in parentheses. F_c = F × shrinkage correction factor of 1.065. G = Average dimensions of diad spores in μm. H = Percent diad spores.

[2] Isotype of *T. dentatum*.

[3] Cited by Fournier as *T. platyderon* Fourn., who also later submerged it in *T. dentatum*.

The reference to the lateral organs as phyllophores rather than petioles is justified on several grounds (Bierhorst, 1974). In creeping forms such as in sect. *Gonocormus*, the apex of the phyllophore produces a lateral axis of appreciable extent. Its apex then dichotomizes and one of the two apices, after a transformation from radial growth to bilateral growth, produces a leaf, or occasionally both apices produce creeping stems. In some other forms, the phyllophore apex divides while still sessile upon the creeping stem, and thus a phyllophore axis is essentially absent. In upright forms such as the *Selenodesmium* species, the phyllophore apex divides to leave behind the so-called axillary bud.

Figure 14 shows the stele at the base of the phyllophore in *T. polystromaticum*. Its structure and symmetry is similar to that of the stem stele. Less than 1 mm from the stem the phyllophore trace divides (*Figs. 15, 16*) to produce two steles of still the same form. The smaller one (right in *Fig. 16*) supplies the bud, and the larger one is continuous with the petiolar strand. The change from stem-type to foliar-type symmetry in the trace is accomplished over a length of about 1 cm. The stele (left, *Fig. 16*) forms a pocket of parenchyma internally but toward the bud trace (*Fig. 17*) and at a slightly higher level those tracheids closing the island of parenchyma disappear (*Fig. 18*). Three protoxylem poles differentiate in the process, two becoming situated each near one of the two ends of the C-shaped trace and one, which is often indistinct, centrally located on the inside of the C.

HYBRIDS OF T. DENTATUM × POLYSTROMATICUM

Based on soral form and lamina structure, *Trichomanes polystromaticum* was not considered more closely related to *T. dentatum* v. d. Bosch than to other species of sect. *Selenodesmium*. But hybrids between the two species apparently exist.

More or less typical *T. dentatum* occurs from Fiji across Polynesia to Tahiti and on New Caledonia. It differs from *T. polystromaticum* in having a more delicate lamina which is but one cell thick, a greater number of cells between ultimate vein endings (*Table 1*), and an involucre considerably longer than wide with better developed, often somewhat flaring lips. In addition, *T. dentatum* has somewhat narrower pinnae and pinnules which overlap only slightly within the plane of the blade. The overlapping character is pronounced in *T. polystromaticum*, to the point where, although the blade is twice compounded, it forms a nearly complete shield (*Figs. 1, 5*).

Five specimens filed as *T. dentatum* in the U. S. National Herbarium suggested in some way *T. polystromaticum* (*Table 1*). All were collected in New Caledonia or the nearby New Hebrides. None bore the broad, short, and apically constricted involucre of *T. polystromaticum*. Four of the five collections had polystromaticous laminae. One (*Buchholz 1209*) exhibited epidermal wall thickenings on the adaxial surface only, a feature not previously reported for any *Trichomanes*. None exhibited the low number of cells between vein endings, a feature which adds appreciably to frond stiffness in *T. polystromaticum*.

An analysis of spore sizes and shapes proved to be more to the point. The spores were mounted directly in glycerine jelly without other treatment. From

slides so made, figures in *Table 1*, column F and G were derived. However, *Bierhorst Fx1* and *NC460* were liquid-preserved collections, and all others were dried. Another preparation of *Bierhorst Fx1* was made by first washing and drying the material. By comparison of the two types of preparations a correction factor of 1.065 was obtained. The average spore diameters of the dried collections were then multiplied by this factor to arrive at F_c in *Table 1*. If any of these measurements are to be compared to figures derived from preparations of spores which were dehydrated, cleared in xylene and mounted in resin, then they should be reduced by 16.7% to compensate for shrinkage by this treatment.

Of the five apparently aberrant collections, four produced some bilateral, diad spores which were often still attached in pairs, as well as normal, trilete, tetrad spores. The diameters of their tetrad spores were intermediate between those of *T. polystromaticum* and more or less typical *T. dentatum*.

The morphological and anatomical evidence allows one to suggest that the five aberrant collections are possible hybrids between *T. dentatum* and *T. polystromaticum*. The spore analysis results when superimposed (see Hickok & Klekowski, 1973) allows for a more positive conclusion of hybridization. The author is not prepared, however, to suggest which hybrids are F_1 and which are F_{1+n}, but he would speculate that there is backcrossing of F_1 hybrids to parental species and complete introgression. An extensive population study on New Caledonia should prove interesting.

Observations by the author on the gametophytes of *T. dentatum, T. obscurum,* and of another still unidentified species of sect. *Selenodesmium* allow the interpretation that physical opportunities for hybridization are particularly high. The filamentous gametophytes theoretically live forever, and they reproduce by gemmae in great abundance. Also, they appear sexually reproductive and not apogamous. The nature of the New Caledonian terrain is also pertinent. It appears to be a classic example of a highly dissected habitat resulting in a multitude of niches. This is reflected by especially high endemism and extremely limited specific ranges of ferns, conifers, and angiosperms.

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Sieve-tube Members in the Stem of Cyathea gigantea[1]

J. J. SHAH and R. L. FOTEDAR*

Cyathea gigantea (Wall. ex Hook.) Holtt. was collected from the Pachmarhi Hills, Madhya Pradesh, India, and was fixed in FAA or 4% formalin solution. After washing with 70% ethanol, the stem was dehydrated, infiltrated, and embedded by conventional methods (Sass, 1958). Sections 6-8 μm thick were stained with a combination of tannic acid, ferric chloride, and resorcin blue (Cheadle, Gifford & Esau, 1953). Mercuric bromphenol blue (Mazia, Brewer & Alfert, 1953) was used to confirm the presence of protein spherules in the sieve elements.

The sieve elements of vascular cryptogams have been defined as sieve cells because there are no specialized sieve areas at their end walls. In *Blechnum orientale* L. stems we have observed some sieve elements in which the pores in the sieve areas at the end walls were measurably larger than those found in the lateral wall sieve areas (unpublished).

In our investigation of phloem in the stem of *Cyathea gigantea* we have observed very large pores at the end walls of some sieve elements (*Figs. A–C*). The pores are either solitary (*Fig. C*) or in groups of two or three (*Fig. B*). The pores are lined with a variable amount of callose. They appear empty, but in some pores protein spherules and cytoplasmic lining can be seen. The pores vary from 2 μm to 5 μm in diameter. Sieve areas with such pores at the end walls can definitely be interpreted as sieve plates, and the sieve elements possessing them as sieve-tube members. In contrast to these pores, the lateral wall sieve area pores are minute, less than 0.8 μm in diameter, and are heavily lined or filled with callose (*Fig. D*). Other sieve elements have small pores at their end walls that are not different from those of the lateral wall sieve areas. These sieve elements are sieve cells.

As far as we know, no sieve plates have been reported in ferns. In *Equisetum* certain sieve elements have transverse or slightly oblique end walls that show considerably large pores. In 1961 Lamoureaux designated these as sieve plates and the cells sieve-tube members (cf. Esau, 1969, p. 365). We conclude that in the stem of *Cyathea gigantea* that we have studied, sieve cells and sieve-tube members are present.

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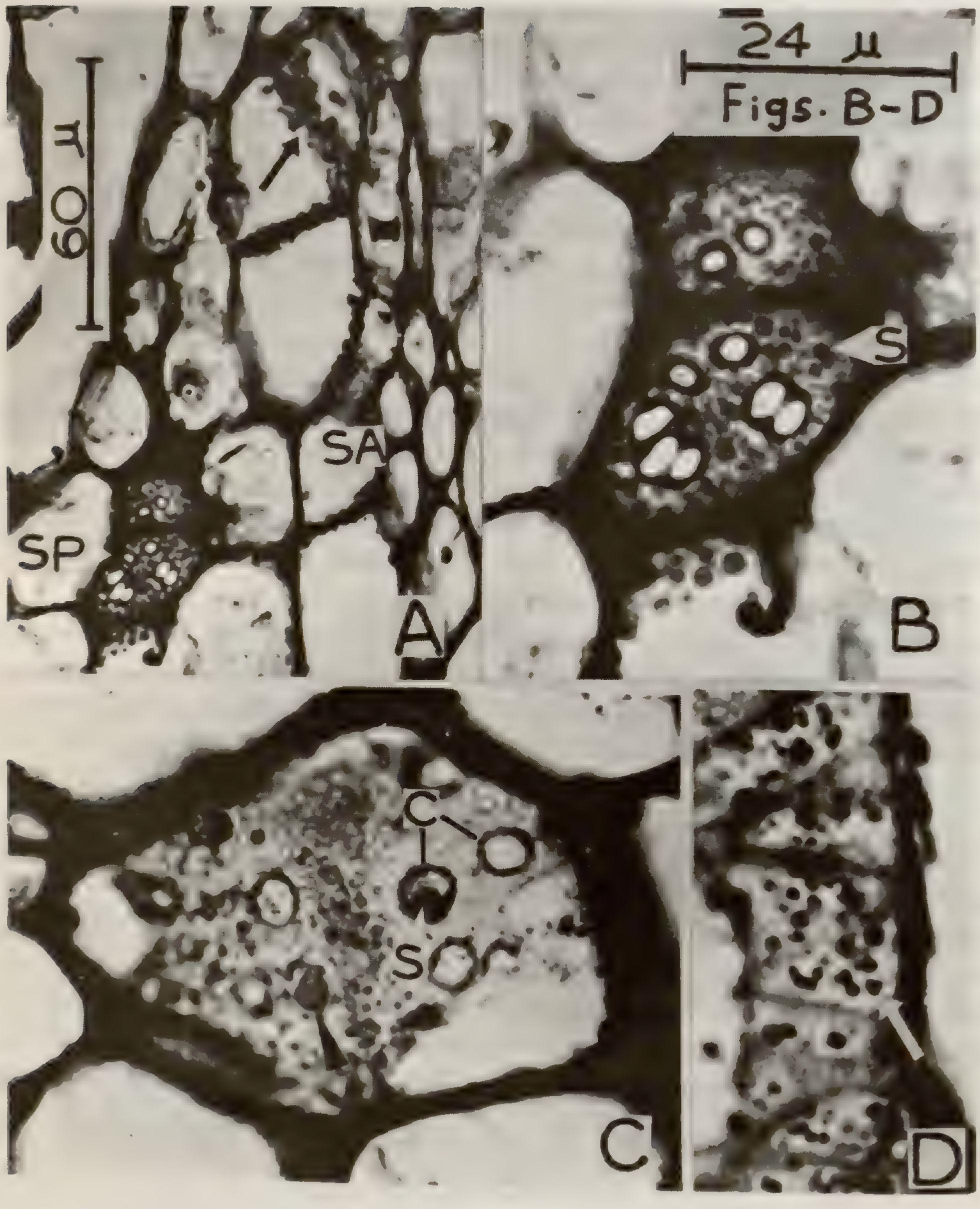

Phloem of *Cyathea gigantea*. FIG. A. Transection showing sieve plate in face view and sieve area in sectional view. Arrow indicates part of a sieve area at the oblique end wall having pores filled with callose. SA = sieve area; SP = sieve plate. FIG. B. Sieve plate in FIG. A, magnified. S = protein spherule. FIG. C. Transection of a sieve plate in face view. Black arrow indicates a protein spherule (in focus) lodged in the pore. C = callose; S = protein spherule. FIG. D. Longisection showing lateral wall sieve areas with callose-filled pores. Arrow indicates a pore heavily lined with callose.

SHORTER NOTES

ADDITIONS TO THE FERN FLORAS OF COLORADO AND NORTH DAKOTA.—A specimen of *Asplenium resiliens* Kunze from Colorado was recently discovered in the University of Kansas herbarium. The label on the sheet reads as follows: "PLANTS OF COLORADO, *Asplenium platyneuron* (L.) Oakes, BACA COUNTY: basalt caprock, confluence of Sand and Gallinas Canyons, tributary to Cimarron River, vicinity of Wilson Ranch, 27 mi. s. Pritchett, T. 35 S., R. 48 W., Sections 5, 8. Alt. 4400 ft. August 6, 1948. *Wm. A. Weber 4351.*" The plant was easily recognized as *A. resiliens* by its uniform fronds, opposite pinnae, and wholly black rachis. This species was previously known from southern Pennsylvania south to Florida, west to Illinois, Oklahoma, New Mexico and Arizona into Mexico (Correll & Johnston, Manual of the Flora of Texas, 1970).

Selaginella rupestris (L.) Spring was collected five miles north of Mountain, Pembina County, North Dakota, on July 25, 1967. A large colony was found on a sandy, brushy ridge in deep woods along the Tongue River. This is the first record for the species in North Dakota, although it has been recorded for surrounding states. Voucher specimens of the collection, *Ralph Brooks 455,* are on deposit in the herbaria of the University of Kansas (KANU) and Kansas State Teachers College (KSTC). In July 1969 the colony was revisited and was found to be in excellent condition and spreading. Additional specimens, *Ralph Brooks 1593,* were collected to further document the earlier findings.—*Ralph E. Brooks, Botany Research Laboratory, University of Kansas, 2045 Ave. A, Campus West, Lawrence, KS 66044.*

LYCOPODIUM CRASSUM IN MEXICO.—Around The pass in the Sierra Juárez between Llano de las Flores and Río Valle Nacional is an interesting station for several species of considerable phytogeographical importance. These species were discussed recently by Sharp and Webster (Amer. Fern J. **61:** 187. 1971). To those taxa previously noted now may be added another: *Lycopodium crassum* H.B.K. I collected a specimen of this *Lycopodium* on December 26, 1970, at about 9500 ft altitude (*Sharp s. n.,* NY). The determination was kindly confirmed by Dr. John T. Mickel. This seems to be the second report for this species north of the páramos of Costa Rica, where it is also found with *Jamesonia*, as it is in the Sierra Juárez. The other collection of *L. crassum* north of Costa Rica was made near the top of Volcán Tajumulco, Depto. San Marcos, Guatemala. The data on this specimen are as follows: Between San Sebastián and top of ridge of Volcán Tajumulco, 16 Feb 1940, 3800–4000 m altitude (*Steyermark 35779,* US). I might add that I have also collected *Jamesonia* on Volcán Tajumulco; evidently in North America *Lycopodium crassum* and *Jamesonia* occur together.—*A. J. Sharp, Department of Botany, University of Tennessee, Knoxville, TN 37916* (Contr. Bot. Lab., Univ. Tenn. N.S. 394).

SCHIZAEA GERMANII REDISCOVERED IN FLORIDA.—*Schizaea germanii* (Fée) Prantl was rediscovered recently in the Loxahatchee National Wildlife Preserve in Palm Beach County, Florida. A few specimens were taken as vouchers (14 Dec 1972, *T. R. Alexander,* BUS, US). Subsequent visits to the area have produced evidence that the population is substantial. The plants grow in the small tree islands that are dominated by *Persea borbonia* and *Ilex cassine*. These islands characterize the Preserve and tend to be of two types: those with margins and interiors covered by a very dense growth of tall ferns and those with the ferns mostly on the margins and the interior open under the tree canopy. The *Schizaea* grows in the latter on old, rotten *Persea* stumps and trunks and in the decomposing litter that is the surface "soil" in these islands.

This species was included in Correll's "A Check-List of Florida Ferns and Fern Allies" (Amer. Fern J. **28:** 16. 1938). It apparently has not been collected in southern Florida in recent decades and is considered rare. Fortunately, this population is protected within the Preserve and cannot be collected without permission. An exact locality is given in Appendix G, South Florida Ecology Study, Recent and Long-term Vegetation Changes and Patterns in South Florida (EVER-N-51). Part 1, Preliminary Report, May 10, 1973. Department of the Interior, by Taylor R. Alexander and Alan G. Crook.—*Taylor R. Alexander, Biology Department, University of Miami, Coral Gables, FL 33124.*

CYSTOPTERIS BULBIFERA NEW TO NEBRASKA.—According to Blasdell (Mem. Torrey Bot. Club **21**(4):1–102. 1963), the range of the Bulblet Fern, *Cystopteris bulbifera* (L.) Bernh., extends as far west as New Mexico and Arizona. However, the distribution within the Great Plains area is quite disjunct according to the specimens cited by Blasdell. This species is found in northwestern Iowa, southeastern Minnesota, and south-central Missouri. Blasdell's rather scanty data for the Great Plains was supplemented by reference to the distributions prepared by R. E. Brooks (pers. comm.), of the University of Kansas, who, after reference to herbaria and considerable collecting in the Plains States west of the Missouri (South Dakota, North Dakota, Nebraska, Kansas), reports the Bulblet Fern only from Roberts County, South Dakota. In June of 1972, I found what I considered to be the first collection of the Bulblet Fern from Nebraska. This fern is common in the recently designated Indian Caves State Park (Richardson County, N½, NW¼, sec. 9, T.3N., R.17E.). It is found in cracks in the heavily shaded sandstone bluffs along the Missouri River and in shallow soil in damp valleys leading to the river. A literature search yielded an unpublished citation of *Filix bulbifera* (L.) Underw. by Howard C. Reynolds (M. S. Thesis, University of Nebraska) in a floristic study of Richardson County done in 1942. It does not appear, therefore, that the fern is an adventive to this region of the state. The habitat of this station is somewhat different from that considered typical (neutral soils associated with limestone) by Blasdell. *Woodsia obtusa* (Spreng.) Torr. and *Cystopteris fragilis* (L.) Bernh. were common associates with the Bulblet Fern. A voucher *(G. J. Anderson 329)* is on file in the Herbarium of the University of Nebraska State Museum (NEB).—*G. J. Anderson, Department of Botany, University of Connecticut, Storrs, CT 06268.*

A NEW COMBINATION IN TECTARIA.—The name *Tectaria irrigua* has been in use for many years, although its source, *Aspidium irriguum* Presl, is a later homonym. The earliest valid name for the species is *Microsorium trifidum* Fée. This necessitates the following new combination:

Tectaria trifida (Fée) M. G. Price, comb. nov.

Microsorium trifidum Fée, Gen. Fil. 269. 1852, basionym.
Aspidium irriguum J. Smith ex Presl, Epim. Bot. 62. 1851, *non* Smith, 1810.
Nephrodium irriguum (Presl) Baker, Syn. Fil. 297. 1867.
Dryopteris irrigua (Presl) Kuntze, Rev. Gen. Pl. **2:** 813. 1891.
Tectaria irrigua (Presl) Copel. Philip. J. Sci. **2C:** 413. 1907; Fern Fl. Philip. **2:** 308. 1960.
Aspidium lamaoense Copel. in Perk. Fragm. Fl. Philip. **3:** 176. 1905.
Dictyopteris lamaoensis (Copel.) v.A.v.R. Mal. Ferns 517. 1909.

The type of *A. irriguum* Presl is *Cuming 31* collected in Luzon. Fée cited the same collection with *M. trifidum*, and I hereby designate the Cuming specimen as lectotype. Some of Cuming's numbers contained mixtures, and this is also possible with no. *31*, for Hooker (Sp. Fil. **5:** 86. 1863) cited it as *Polypodium menisciicarpon,* which is now understood to be a synonym of *Tectaria siifolia* (Willd.) Copel. But even if Hooker were correct in regard to his own specimen, Fée's diagnosis is more appropriate to what has been called *T. irrigua*, and I have no qualms about accepting his name. Holttum (Nov. Bot. Inst. Bot. Univ. Carolin. Prag. **1968:** 28. 1969) reported that specimens at Kew (where Hooker's herbarium is housed) of *Cuming 31* agree with Presl's type of *A. irriguum*.

T. trifida is always found at low elevations anchored to boulders in stream beds within the flood zone. It occurs with certainty in only Luzon and Samar, Philippines.

Closely related are two species described from Sarawak specimens, *T. lobbii* (Hook.) Copel. and *T. subdigitata* (Baker) Copel. Both differ from *T. trifida* by large, firm, persistent indusia and longer, narrower pinnae. Furthermore, *T. lobbii* is more deeply divided and has the main veins more oblique than *T. trifida*. In the event that any of these taxa are combined at the species level, Fée's name is the earliest.—*M. G. Price, Dept. of Botany, U. P. at Los Baños, College, Laguna, Philippines.*

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The Natural History of Ophioglossum palmatum in South Florida[1]

MICHAEL R. MESLER*

Of the sixty or more species in the Ophioglossaceae, only *O. pendulum* L. and *O. palmatum* L. are epiphytes. Although some authors (Chrysler, 1941; Eames, 1936, fig. 78) have regarded these species as relatively primitive in the genus and have envisioned a reduction series culminating in the more diminutive terrestrial species, others have suggested that they are advanced in most respects (Bower, 1911, 1926; Wagner, 1952). Because detailed information about the gametophytes, spore wall sculpturing, stem structure and development, and venation pattern —among other characters—is not available for most species in the genus, strong adherence to either hypothesis serves little purpose at the present time. Nevertheless, the derivative state of the epiphytic habit in *Ophioglossum* is supported by its extremely low frequency of occurrence in the genus and the family and the unique frond architectures displayed by both *O. pendulum* and *O. palmatum*.

Numerous discussions of the peculiar features of these epiphytes, as well as speculations about their evolution, have dominated the literature dealing with them, but little has been reported about their natural history and ecology. For this reason, in this paper I would like to relate observations on the natural history of a population of *O. palmatum*, the Hand Fern, in southern peninsular Florida. In addition, I shall attempt to place these observations into the context of the natural history of *O. palmatum* as it occurs in other parts of its range, as well as that of *O. pendulum* in the Old World tropics.

Ophioglossum pendulum is found throughout the Old World tropics, except for Africa, and is also found in Hawaii (Christensen, 1932; Clausen, 1938, p. 117). It has elongate, ribbon-like blades up to 4 m long and 9 cm wide which often fork in large specimens. Horner (1958), Graf (1970), and Carlquist (1970) each illustrate this species. Each leaf bears one fertile spike which may exceed 50 cm and which is inserted medianly on the sterile portion of the leaf blade. Mature leaf blades are perpendicular to the supporting surface (Wagner, 1952), and stomates are present on both leaf surfaces.

Ophioglossum palmatum is found in the New World tropics, and is also found in South Vietnam, Madagascar, the Seychelles, and Réunion (Christensen, 1932; Tardieu-Blot, 1953; Clausen, 1938, p. 114; Wieffering, 1964). It has blades up to 45 cm long and 30 cm wide which are broad at the base and are divided into a variable number of distal lobes. The leaves of *O. palmatum* have been described as palmately or dichotomously lobed, but no ontogenetic evidence has been presented to support either view. Similarly, the leaf ontogeny of *O. pendulum* is unknown. Craighead (1963) and Troll (1933) illustrate the species. Each leaf bears from one to 15 or more fertile spikes up to 7 cm long which are inserted at the apex

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[1] I am grateful to the following individuals for their generous help: C. E. Delchamps, W. H. Wagner, Jr., J. G. Bruce, D. Beale, M. Hair, F. C. Craighead, Sr., M. G. Price, and R. G. Stolze. I am especially indebted to Dr. Delchamps for introducing me to the Hand Fern in Florida.

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FIG. 1. *Ophioglossum palmatum* growing from Cabbage Palmetto in Collier County, Florida, × ½.

of the stipe and along the margin of the blade. Mature leaf blades are parallel to the supporting surface, and stomates are present only on the abaxial surfaces. Contrary to the opinion of Nakai (1925) and figure 78 in Eames (1936, p. 118), the leaves of epiphytic plants of *O. palmatum* are arching or pendent, but not erect, at maturity. Reports of erect leaves are presumably based on rare, terrestrial collections. Both species may rarely occur terrestrially, growing on rotting logs or moss-covered rocks.

Although the two species are generally geographically separate, both have been collected in Madagascar, the Seychelles, and Indochina. Both species have been divided into subspecies or varieties on the basis of leaf size, shape, and texture. These subdivisions are not convincing, however, because intermediate plants occur throughout the range of each species (Clausen, 1938, 1954; Horner, 1958; Wieffering, 1964). A plant resembling *O. palmatum* and perhaps constituting a distinct species has been reported from Zaire (Belgian Congo) by Taton (1944).

A large population of *O. palmatum* located in Collier County, Florida, was investigated in January 1971 and 1972, in March 1972 (dry season), and in July 1973 (wet season). The habitat is a mixed hardwood association bounded on one side by a river and described as a "palmetto hammock" by F. C. Craighead, Sr. (1973, pers. comm.). The dominant trees are Red Maple, Live Oak, Bald Cypress, and the Cabbage Palmetto. The climate is strongly seasonal: 60%–80% of the yearly precipitation falls in a five-month period (May through October), and in some years the monthly rainfall during the dry season may be negligible (Craighead, 1971). During the rainy season the entire area is inundated, but in the dry season most of the ground is exposed. The proximity of the river prevents total drying of the substrate during the dry months, however, and probably accounts for the fact that extensive burning has not occurred in the area in recent years.

At the locality, the Hand Fern was observed growing only on the arborescent Cabbage Palmetto, *Sabal palmetto* (Walt.) Lodd. ex Schultes. The stems of the palm are covered by a mantle of overlapping, fibrous, persistent leaf bases that collect falling debris (*Fig. 1*). Each leaf base develops a vertical cleft due to expansion forces created by the primary expansion of the trunk (Tomlinson, 1962). Although the trees are at least partially resistant to fire, as indicated by the large numbers of charred but living plants easily observed on a drive through Everglades National Park, the leaf bases are highly flammable. Even without burning, however, older leaf bases gradually decay, loosen, and fall from the trees.

Ophioglossum palmatum lives in the humus that accumulates underneath the leaf bases of the palmettos. Although plants could be observed at various points along the trunks of the palmettos, from near the bases to just below the crown, they are generally restricted to the upper parts of the palmettos. The stem and root system of a particular plant are completely covered and can only be observed after two or three layers of the overlapping, tightly appressed leaf bases have been removed. Mature plants may bear as many as six leaves, all or some of which are fertile. A single leaf commonly produces three to six erect fertile spikes, but larger leaves may bear as many as ten. Although leaves are present on the plants

throughout the year, they are not produced continuously; the peak of leaf development occurs during the summer rainy months, and the sporangia mature between December and May. The fleshy, tuberous stems (1.5+ cm in diameter in older plants) are covered with fine, light brown hairs. Several large, branching roots grow from a stem, radiating for considerable distances under the palmetto leaf-base mantle, in some cases penetrating decaying leaf-base tissues. Rarely, actively growing roots were found attached to inactive, necrotic stems without leaves, and in two instances living roots were found with apparently no stem attachment whatsoever. The succulent character of the roots of the Hand Fern is emphasized by observation of squirrels feeding on them during severe dry weather (W. R. Llewellyn in Craighead, 1963).

Although Small (1938, p. 368) states that in peninsular Florida *O. palmatum* is found "On trees, often among the bases of the leaves of the cabbage tree. . . ," I have been unable to find herbarium sheets or other records documenting its occurrence on any other tree in the state. F. C. Craighead, Sr. and C. E. Delchamps, both of whom have had extensive field experience in southern Florida, report that they have encountered the Hand Fern only on the palmetto.

In other parts of its range, *O. palmatum* is not confined to the Cabbage Palmetto, nor in fact to other palms. Its preference for the Palmetto in southern Florida appears to be the result of the pronounced wet–dry seasonality and the inability of its unprotected sporophytes and gametophytes to withstand xeric epiphytic conditions. The sporophytes are mesophytic. Although the succulent, tuberous stems, roots, and leaves may serve as water reservoirs, there are no obvious structural modifications for rapid uptake of water or for reducing water loss during periods of stress. When sporophytes are removed from the palmettos and left exposed in the air, their leaves begin to wilt almost immediately. Similarly, the slow-growing, parenchymatous gametophytes are highly susceptible to damage by desiccation.

It is not surprising that throughout most of its range *O. palmatum* is confined chiefly to tropical montane sites where moist conditions prevail all year around or with only minor interruption during mild dry seasons (Martens & Galeotti, 1842; Maxon, 1926; Proctor, 1953; Tryon, 1960; W. H. Wagner, Jr. and L. D. Gomez, 1971, pers. comm.; R. G. Stolze, 1973, pers. comm.). Plants of the Hand Fern from these moister regions have most commonly been observed on the branches of various species of dicotyledonous trees, but have also been seen growing on palms, rocks (Martens & Galeotti, 1842), and from the root masses of bromeliads (Wagner, 1974, pers. comm.). The stems and roots of the Hand Fern are embedded in moist humus that accumulates among epiphytic bryophytes, other pteridophytes, orchids, and bromeliads. The requirement for a continuously moist substrate is illustrated by observations of Tryon (1960) in Peru. He noted that when a branch supporting plants of the Hand Fern fell from a tree into a more exposed position, the plants died after a mild dry season.

Specialized epiphytes, such as orchids and tillandsioid bromeliads, are common in southern Florida. But the relatively severe dry seasons characteristic of the area would appear to militate against the occurrence of a mesophytic epiphyte like

O. palmatum. Nevertheless, the Hand Fern was apparently once present at many localities in southern Florida (Small, 1938). The explanation for this appears to lie in the ability of the species to colonize the only microsites that provide a constantly moist substrate; namely, the interfaces between the trunks and persistent leaf bases of the Palmetto. Not all palmettos, however, offer an equally suitable environment. A survey at the Collier County locality indicated that the condition of the leaf base mantle (relatively intact and tightly held versus decayed and loose) determines the moisture content of the humus beneath the leaf bases and, thereby, influences the ability of the Hand Fern to become established. This explains the greater number of Hand Fern plants observed on the upper, younger parts of the Palmettos. Gametophytes occur only in the most moist microsites, but the sporophytes are slightly more tolerant of drier conditions. Plants were never observed, however, on exposed trunks which had fallen leaf bases or which had been damaged by fire.

The Hand Fern has disappeared from many of its previous localities in southern Florida (Small, 1938) and now is perhaps in danger of extinction there. In a letter to M. A. Chrysler (Chrysler, 1941), J. K. Small wrote "Forty or fifty years ago one could go to the edge of the Everglades back of Miami and collect it by the wagon load. Today not a leaf can be found there." Part of the explanation for the disappearance of the species from southern Florida has been extermination of colonies by collectors. For example, Dr. Craighead (1973, pers. comm.) reports that prior to the opening of Mahogany Hammock (Everglades National Park) to the public, as many as 40 to 50 Cabbage Palmettos bore plants of the Hand Fern. Subsequently, "Most of the orchids were soon removed by collectors and finally the Hand Fern. I then searched the entire hammock and did not find a single Hand Fern plant. Later, several more surveys were made with the same results." The superficial resemblance of the Hand Fern to *Platycerium* has earned for it the additional local name of "Dwarf Staghorn" and accounts for collections by those seeking to grow it in cultivation. The species, however, has not had even the limited success in cultivation as that enjoyed by *O. pendulum* (see Graf, 1970).

More important than the effects of over-collection in understanding the decline of *O. palmatum* are the recent extensive drainage and water diversion activities in the Everglades. These programs have had the effect of prolonging the dry season to the extent that soils that previously remained moist until the onset of the summer rains were allowed to dry. The result has been a marked increase in the frequency and severity of fires (Craighead, 1971, 1973). Fires destroy the leaf bases of the Palmettos and thereby the only available habitat for the Hand Fern in the area. Thus, *O palmatum* persists today only in moist hammocks that have escaped fire (Craighead, 1963).

More is known about the natural history of *Ophioglossum pendulum* than of *O. palmatum*, perhaps because it is more common through its range and is a more conspicuous element of the vegetation. The species is confined to moist tropical regions (lowlands or montane) characterized by an almost even distribution of rainfall throughout the year. Short "dry" seasons do occur, however, as well as daily fluctuations in the amount of rainfall input and humidity (Walter, 1971). For example, although at Tjibodas (Java) in some years there may be as many as 300

rainy days, rarely are there three weeks without rain (Went, 1940). In addition, humidity decreases at higher levels in the forest, falling as low as 40% at 18 m (Schimper & Faber, 1935). Consequently, the mesophytic epiphyte *O. pendulum*, often growing in open forests, must rely on a humus substrate that acts as a water reservoir and buffer against desiccation as well as a source of nutrients.

Holttum (1954a, p. 41) reports that in the lowlands of Malaya, *O. pendulum* "is sometimes found on tree trunks where humus has collected, but more often on palms which have persistent leaf-bases." Wagner and Grether (1948a) observed small plants growing in moss at the bases of Sago Palms in the freshwater swamps of the Admiralty Islands. At high elevations (1000–1500 m) in the Philippines, plants grow "in the root masses of *Asplenium cymbifolium* Christ and also from sheltered crevices in mossy trunks and branches from mats of bryophytes and Hymenophyllaceae." (M. G. Price, 1974, pers. comm.). *Ophioglossum pendulum* has perhaps most often been observed growing from the accumulation of humus at the bases of plants of *Asplenium nidus* and *Platycerium* spp. (Holttum, 1954a,b; Wagner & Grether, 1948a,b; Wieffering, 1964; M. G. Price, 1974, pers. comm., Went, 1940; Campbell, 1907). Holttum (1938) suggests that hardy epiphytes like *Asplenium nidus* and *Platycerium coronaria* colonize relatively exposed, xeric positions in the canopy and make possible subsequent growth of mesophytic epiphytes like *O. pendulum*. Larger plants of *O. pendulum* compete with *Platycerium* plants for nutrients and moisture and in this way may eventually kill the *Platycerium* (Holttum, 1954b). Campbell (1907, p. 140) observed in Ceylon that "*O. pendulum* was found to be fairly abundant near Hanwella, but the weather was very dry, so that the masses of humus in which the plants were growing were dry as powder and no prothallia could be procured." This observation suggests that as with *O. palmatum*, the gametophytes of *O. pendulum* are less resistant to dry conditions than the sporophytes.

Both *Ophioglossum palmatum* and *O. pendulum* are relatively unspecialized, mesophytic epiphytes. Both species require a more or less constantly moist humus substrate for establishment and maintenance of growth. Under conditions of relative drought, such as the seasonal climate of southern Florida or close to the canopy in the Malayan evergreen forest, plants are restricted to microsites with humus masses protected against desiccation. In Florida, it is the leaf-base mantle of the Cabbage Palmetto that affords the necessary protection, while in Malaya it is often the bases of nest or bracket epiphytes. In addition to providing moisture and nutrients, the humus provides a substrate for the endophytic fungus essential to the growth of the gametophytes and young sporophytes and satisfies the probable dark requirement for spore germination (see Whittier, 1973).

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Photosynthesis and Respiration of Ferns in Relation to Their Habitat

HEW CHOY-SIN and WONG YIK SUAN*

There are at least 500 species of ferns in Malaysia and Singapore, and these plants form a conspicuous part of the local flora. The reason for their abundance lies in the particularly favorable climate of this part of the world. Holttum (1954) has divided the ferns of Malaysia and Singapore into various classes according to the conditions under which they grow: terrestrial sun ferns, terrestrial shade ferns, epiphytes of sheltered places, epiphytes of exposed places, rock and river-bank ferns, aquatic ferns, and mountain ferns. The fact that ferns grow in a great diversity of habitats makes them very interesting plants for physiological and ecological studies.

Interest in the physiological studies of ferns has been centered mainly in the growth and development of fern gametophytes (Allsopp & Rao, 1969; Bloom & Nicols, 1972; Miller & Miller, 1961; Raghavan, 1965; Sobota & Partanen, 1966), spore germination (Raghavan, 1971), and the changes accompanying the conversion of aquatic to land forms of *Marsilea* (Allsopp, 1955; Gaudet, 1963, 1965). More recently, the role of light in the interrelated processes of morphogenesis and photosynthesis of fern gametophytes has also been investigated (Donaher & Partanen, 1971). However, very little work has been done on photosynthesis and respiration of fern fronds, particularly in relation to their adaptations to different habitats.

PLANT MATERIALS

Angiopteris evecta Hoffm. was collected from Bukit Tamah Nature Reserve, Singapore. Plants were potted and grown in a shady place for two months before the fronds were used for experiments. Plants of *Marsilea crenata* Presl were grown with submerged roots in a large water tank in an open place. A layer of soil for the anchorage of the roots was laid on the floor of a tank. *Adiantum philippense* L. was grown in a semi-shady place. *Gleichenia linearis* (Burm.) Clarke, *Nephrolepis biserrata* (Swartz) Schott, *Drymoglossum piloselloides* Presl, *Davallia* sp.; and *Asplenium nidus* L. were collected from various terrestrial and epiphytic habitats around the University campus.

Fronds were cut just before the experiments and taken to the laboratory where the stipes were recut under water to prevent possible blockage of the xylem with air, thereby affecting transpiration. The stipes were then placed in water in a small polyethylene bag. Together they were transfered and placed in the central plane of a lucite photosynthesis chamber. The chamber was positioned vertically, and light was supplied from one side of the chamber. The set up for CO_2 gas exchange analysis using a Beckman infra-red CO_2 analyser was similar to those previously described (Wong & Hew, 1973).

A closed system was used to measure the CO_2 compensation point and to study the effect of CO_2 concentration on apparent photosynthesis, while an open sys-

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tem was used to determine the steady rate of apparent photosynthesis at various light intensities.

To isolate glycolic acid oxidase, fronds (2 gm) were cut and homogenized in a Waring blender. Isolation medium contained 0.05M Tricine buffer (pH 8) with polyvinyl pyrrolidone (0.5 gm) added. The homogenate was filtered through eight layers of cheese cloth and then centrifuged at 6000 $\times g$ for 1 min. The supernatant fluid was used as a crude enzyme extract. Oxygen uptake by glycolic acid oxidase was measured with a Clark type O_2 electrode. (Wong & Hew, 1973). Reaction medium contained 10^{-2} M Tricine buffer pH 8. α HPMS (Hydroxy 1-2-pyridine methane sulfonic acid) was used to inhibit glycolic acid oxidase activities.

All measurements were repeated at least twice with different plants.

PHOTOSYNTHESIS, PHOTORESPIRATION, AND DARK RESPIRATION

For all the ferns studied except *Drymoglossum piloselloides*, an increase of light intensity increased the rates of apparent photosynthesis (*Figs. 1–8*). For *Gleichenia* and *Nephrolepis*, light saturation was reached about 8×10^4 erg cm $^{-2}$ sec $^{-1}$ with a rate of 4 to 6 mg CO_2 hr $^{-1}$ gm $^{-1}$ fresh weight (*Table 1*). Fronds of *Adiantum* and *Marsilea* have apparent photosynthetic rates similar to those of terrestrial sun ferns. The only difference was that they saturated at 4×10^4 erg cm $^{-2}$ sec $^{-1}$. Very low rates of apparent photosynthesis were obtained for *Asplenium* and *Angiopteris*. Apparent photosynthesis saturated at 2×10^4 erg cm $^{-2}$ sec $^{-1}$. Light compensation points were in the region of 1 to 4×10^3 erg cm $^{-2}$ sec $^{-1}$ for all the ferns except *Drymoglossum*.

TABLE 1. PHOTOSYNTHESIS, PHOTORESPIRATION AND RESPIRATION OF SOME COMMON FERNS.

Species	*Exposure & Habitat*	*P max*[1]	*Dark Respiration*[1]	*Photorespiration*[1]
Gleichenia linearis	Sun, terrestrial	5.0, 6.0	1.0, 0.8	1.8, 1.7
Nephrolepis biserrata	Sun, terrestrial	4.2, 4.2	1.0, 0.6	2.1, 1.9
Adiantum philippense	Shade, terrestrial	4.0, 5.2	0.5, 0.5	—
Marsilea crenata	Sun, aquatic	5.0, 5.0	0.5, 0.7	—
Angiopteris evecta	Shade, terrestrial	1.5, 1.5	0.2, 0.4	0.8, 1.0
Asplenium nidus	Shade, epiphytic	1.1, 1.1	0.2, 0.25	0.9, 0.8

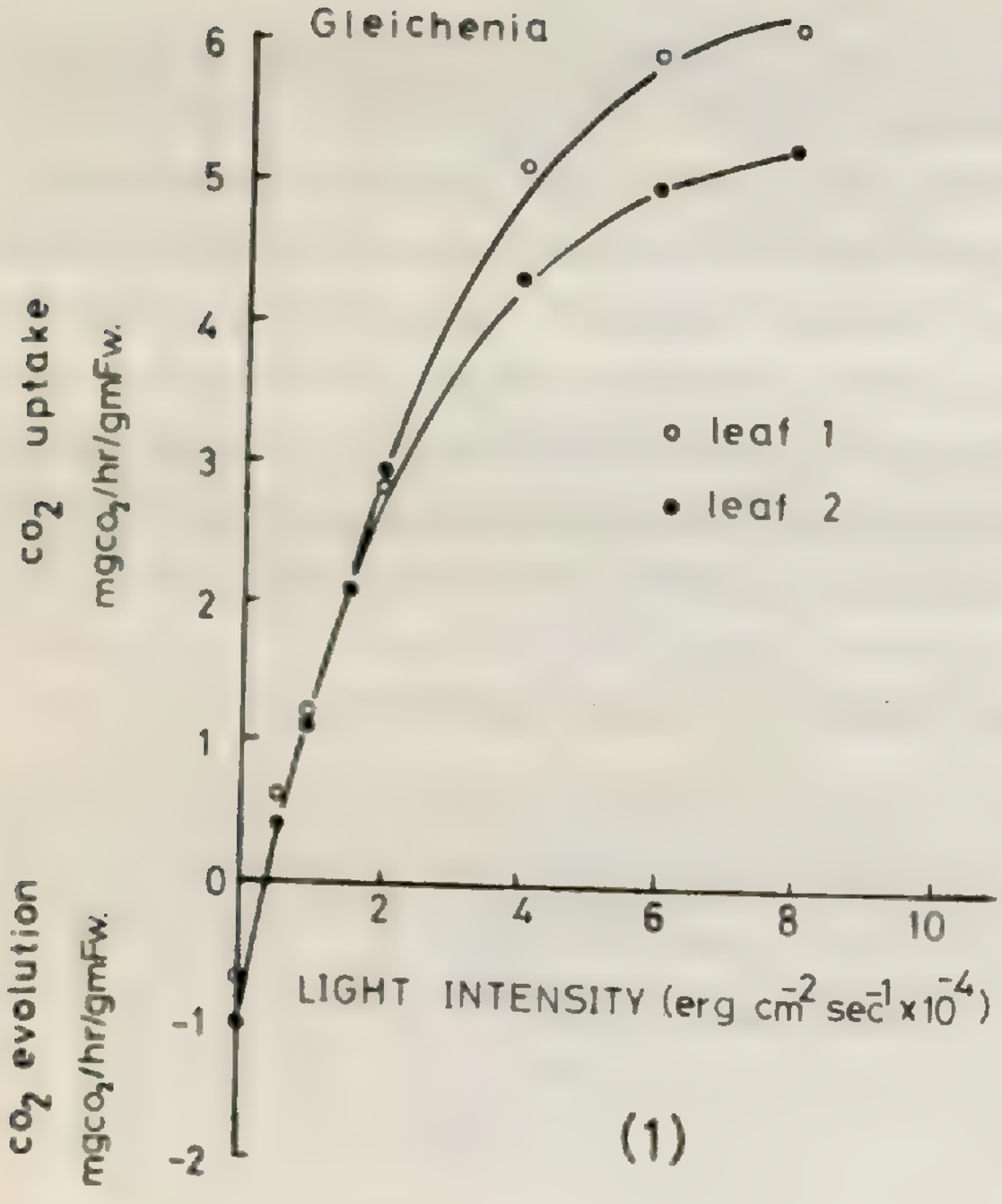
[1]Two replicates; the values are given in mg of CO_2 per hour per gm fresh weight.

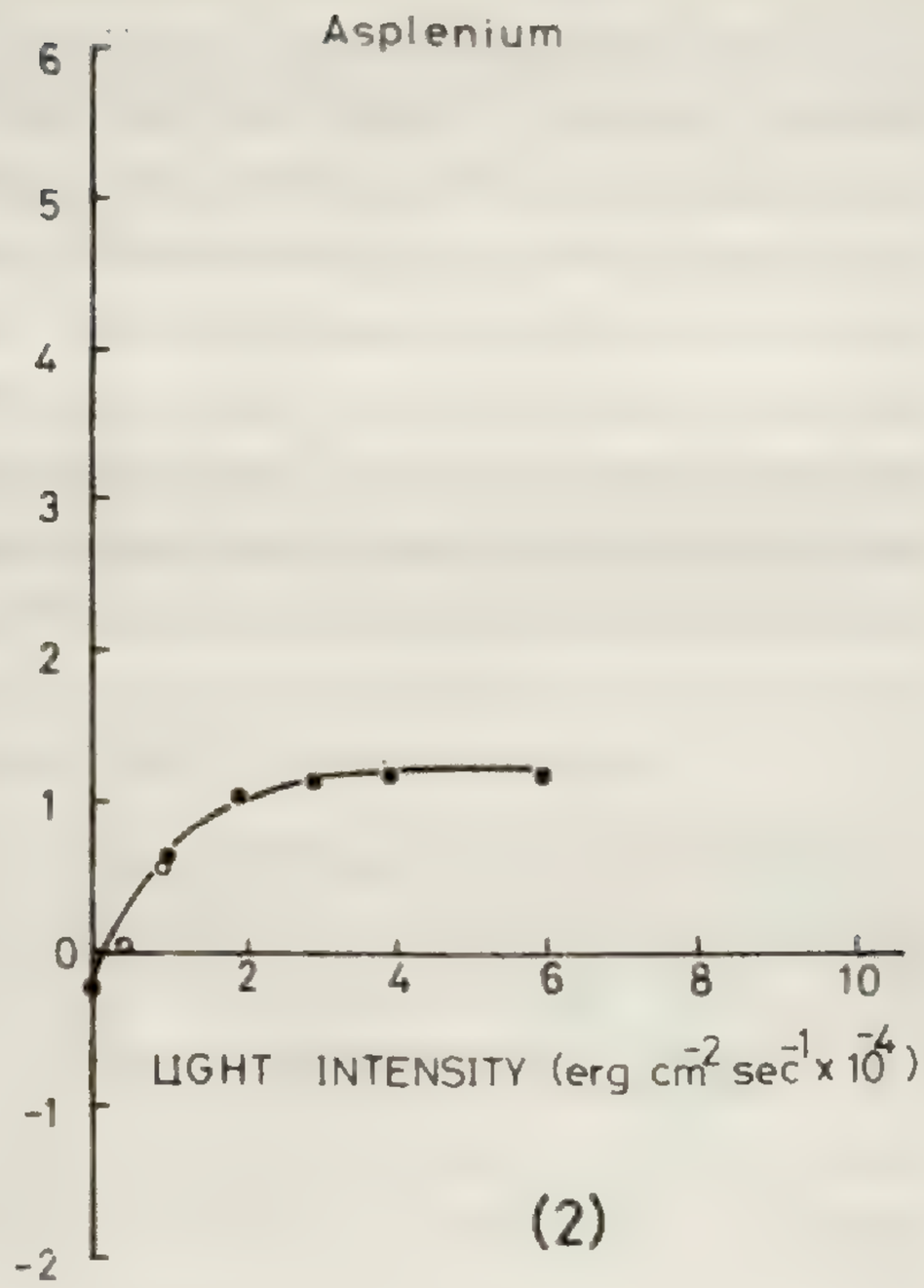
In *Drymoglossum*, there was no CO_2 uptake at any light intensity. Instead, there was CO_2 evolution which was suppressed by light.

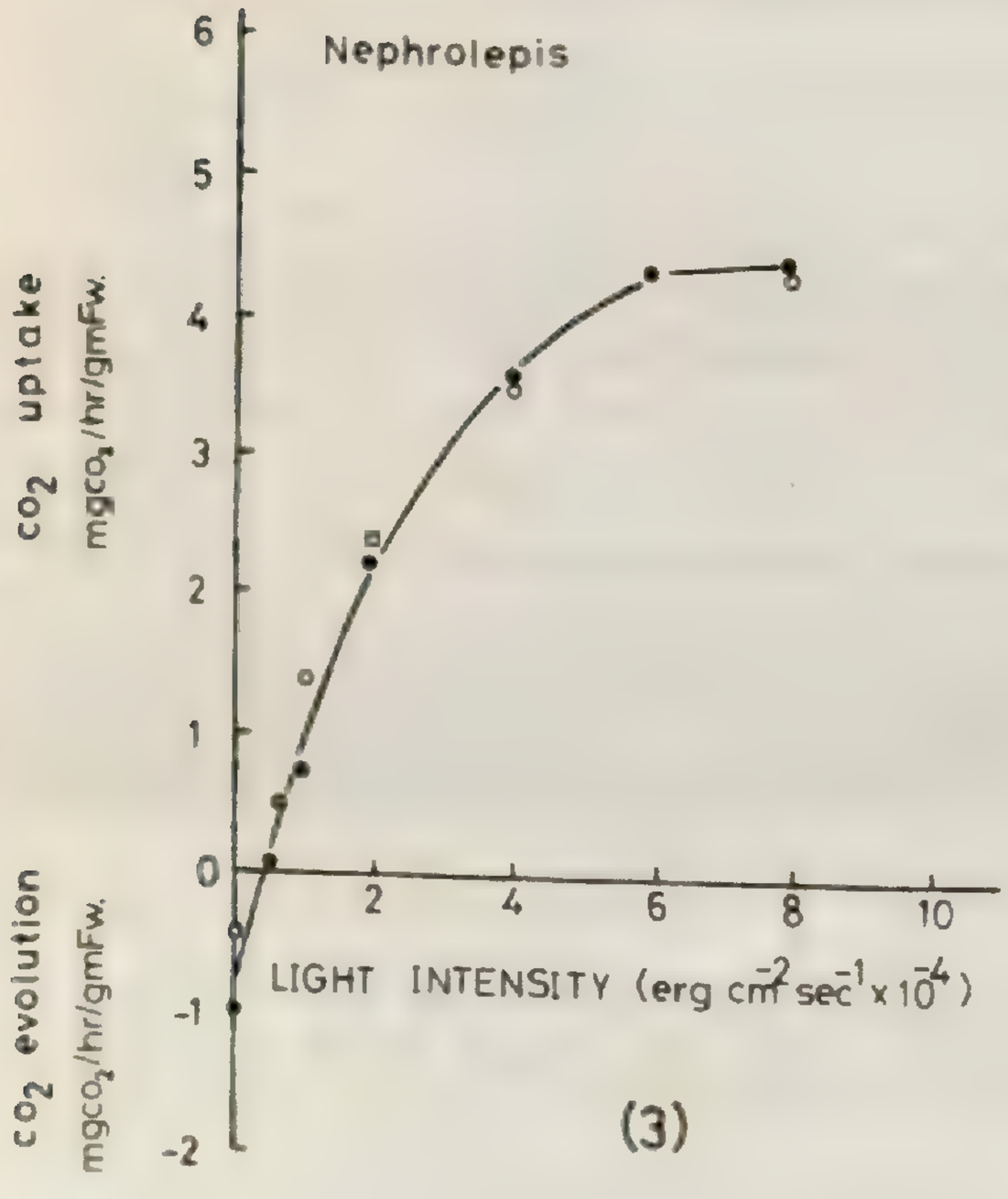
The effects of CO_2 concentration on apparent photosynthesis of four ferns is shown in *Figs. 9–12*. There was a linear relationship between CO_2 concentration and apparent photosynthesis for both the sun (*Figs. 9, 10*) and shade ferns (*Figs. 11, 12*) up to about 200 ppm.

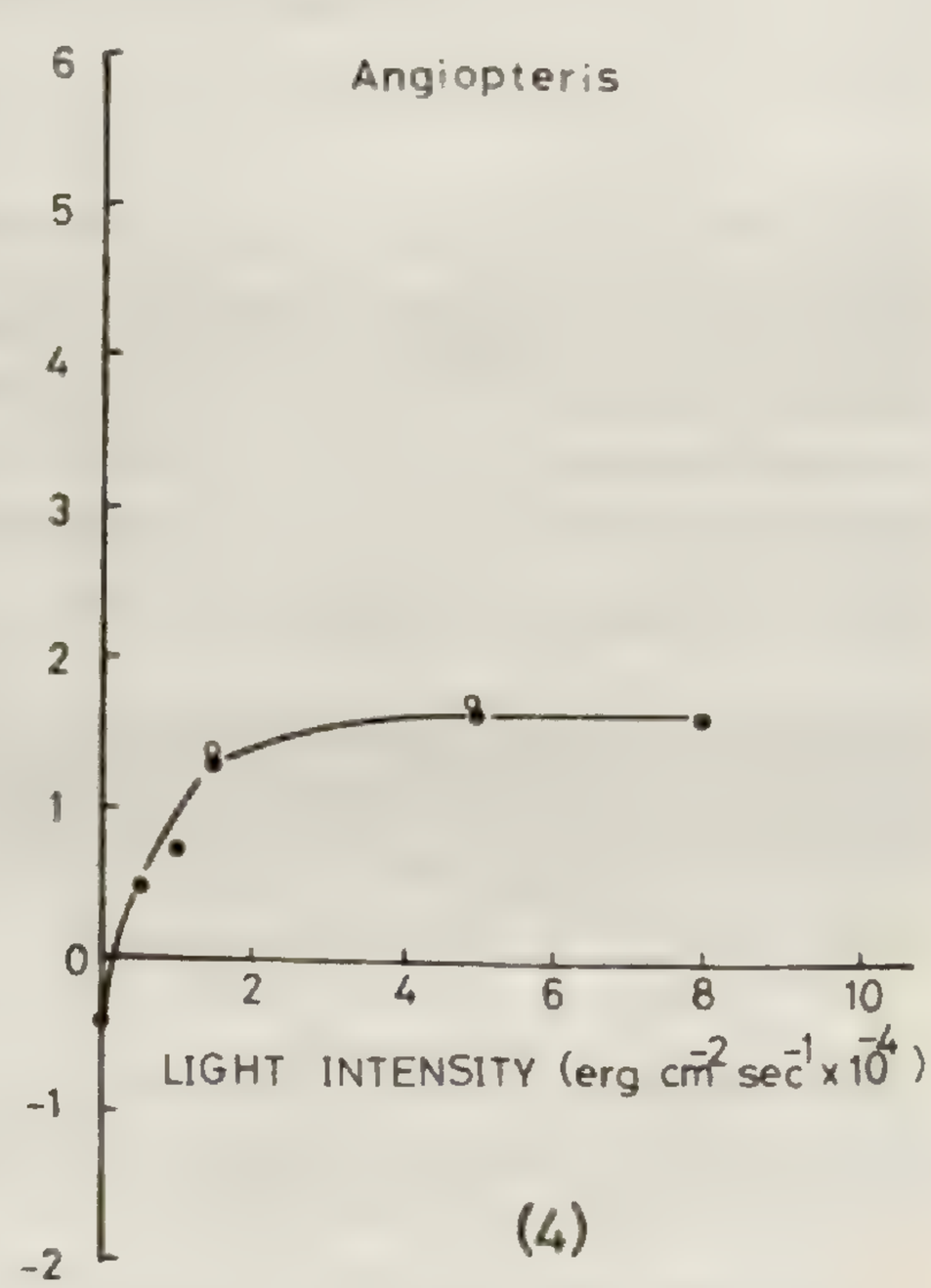
Postillumination CO_2 outburst was observed in both sun and shade ferns. This was followed by a more steady but lower rate of dark respiration (*Figs. 9–12*).

Photorespiration obtained by extrapolating the CO_2 concentration verus apparent photosynthesis graph to zero CO_2 concentration (Hew et al., 1969) was found

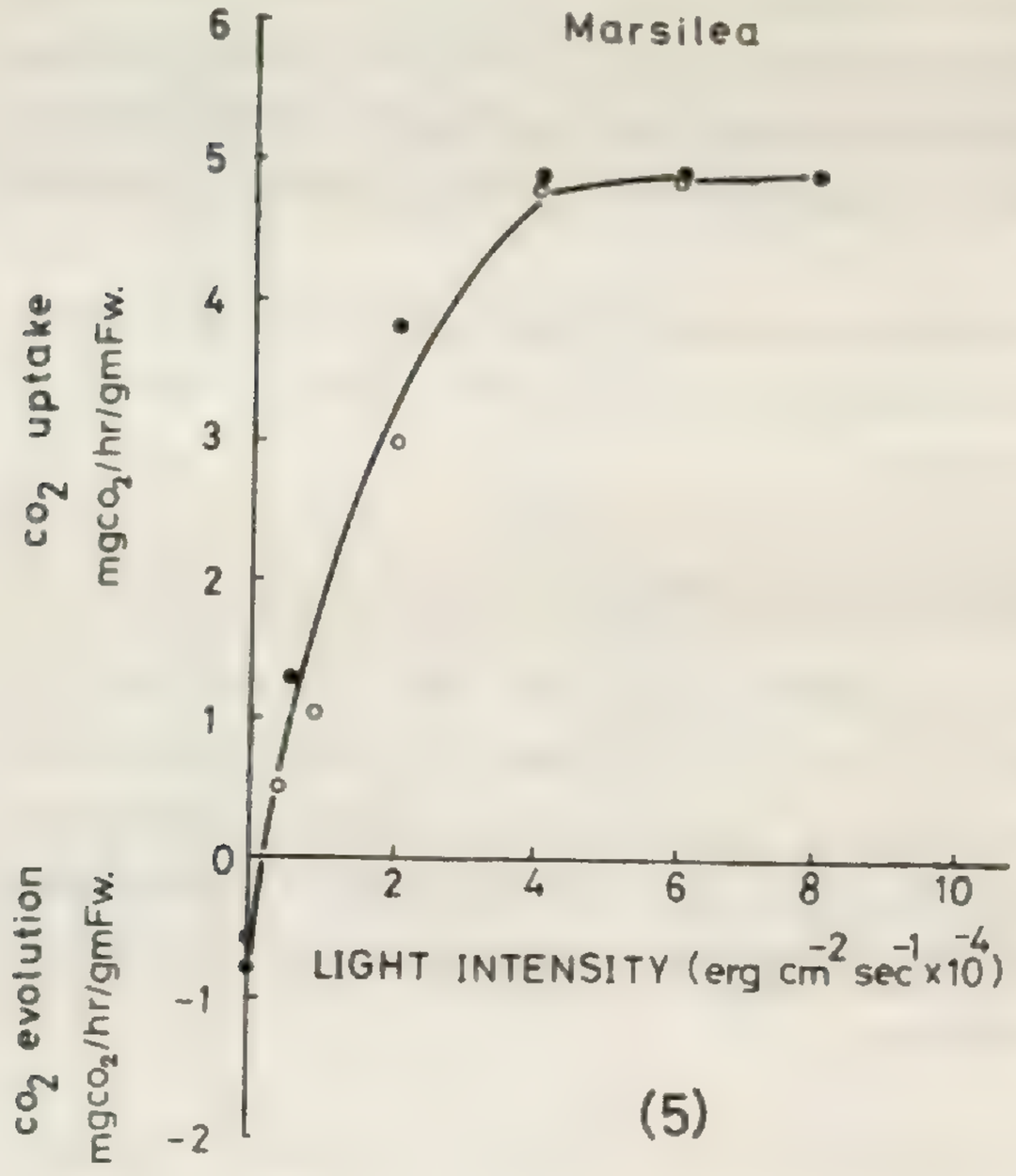


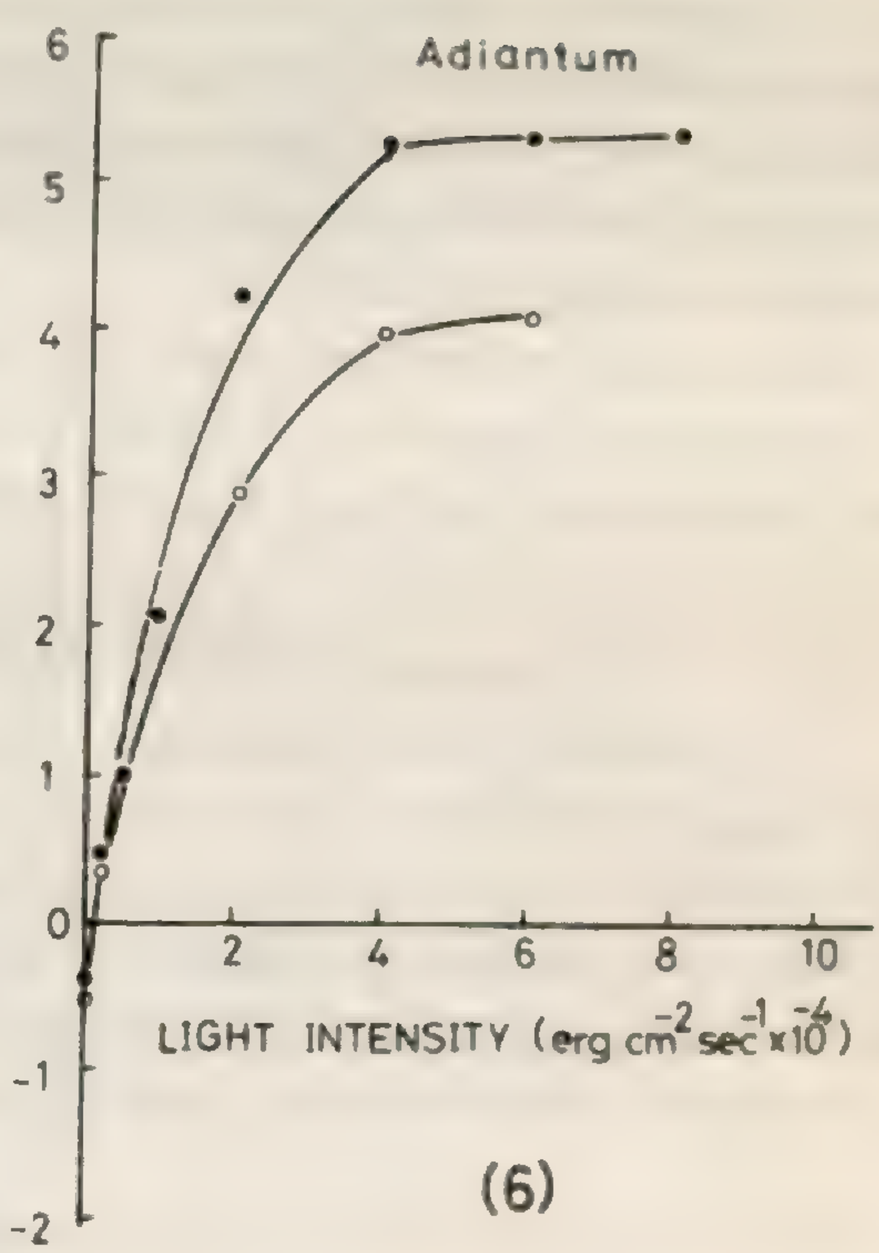


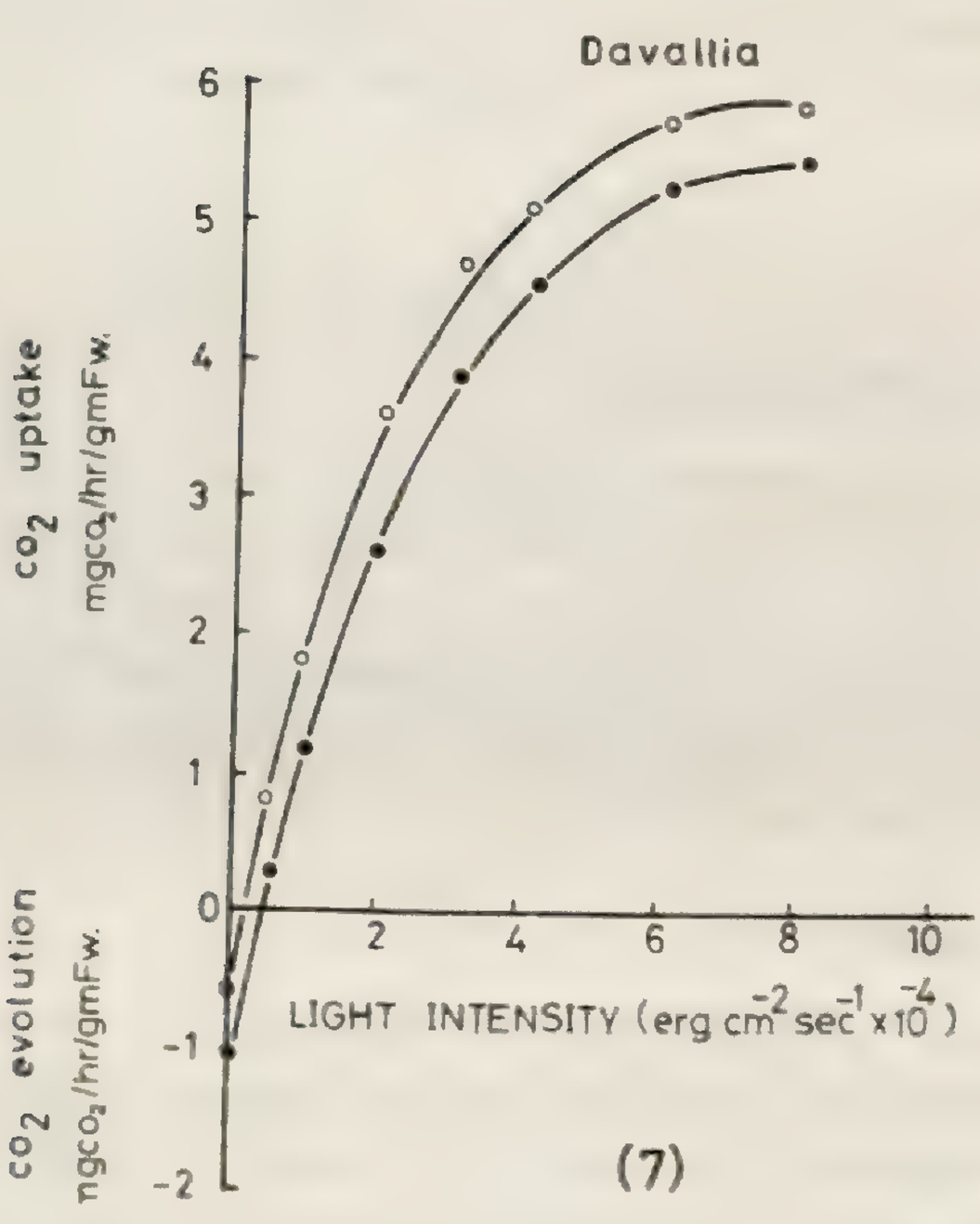


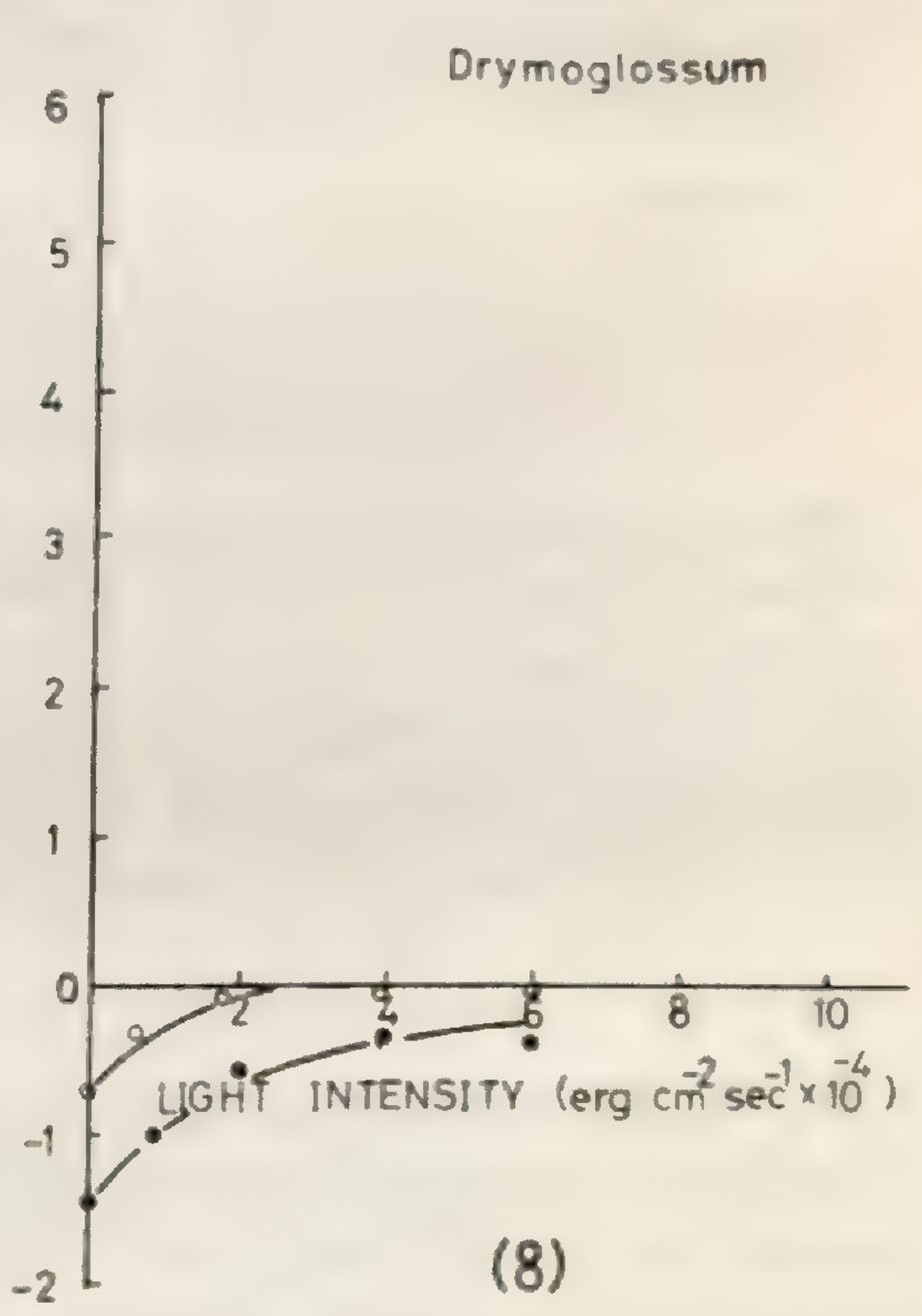


The effect of light intensity on apparent photosynthesis. FIG. 1. *Gleichenia*. FIG. 2. *Asplenium*. FIG. 3. *Nephrolepis*. FIG. 4. *Angiopteris*.









The effect of light intensity on apparent photosynthesis. FIG. 5. *Marsilea*. FIG. 6. *Adiantum*. FIG. 7. *Davallia*. FIG. 8. *Drymoglossum*.

to be generally higher than dark respiration (*Table 1; Figs. 9–12*). Ferns with high photosynthetic rates also have high photorespiratory and dark respiratory rates. In sun ferns, rates of dark respiration were one-tenth to one-fourth of the photosynthetic rate, but in shade ferns the rates of dark respiration were about one-fifth of the photosynthetic rates.

Table 2 shows a survey of CO_2 compensation points in fronds of different ferns. They ranged from 40 to 75 ppm CO_2 concentration, with shade-loving ferns such as *Angiopteris* having a slightly higher value.

GLYCOLIC ACID OXIDASE ACTIVITIES

To ascertain the presence of photorespiration in ferns, the occurrence of glycolic acid oxidase activities was studied. *Figure 13* shows a typical tracing of O_2 uptake by *Marsilea* frond extract. Addition of potassium cyanide inhibited all known oxidases except glycolic acid oxidase. Upon the addition of sodium glycolate, there was a rapid O_2 uptake which was strongly inhibited by α HPMS, a competitive inhibitor of glycolic acid oxidase.

TABLE 2. A SURVEY OF CO_2 COMPENSATION POINTS OF SOME COMMON FERNS.

Species	*Exposure & Habitat*	*CO_2 compensation point* (ppm)
Gleichenia linearis	Sun, terrestrial	40, 47[1]
Nephrolepis biserrata	Sun, terrestrial	52, 48
Adiantum philippense	Shade, terrestrial	43, 46
Marsilea crenata	Sun, aquatic	50, 51
Angiopteris evecta	Shade, terrestrial	70, 61
Asplenium nidus	Shade, epiphytic	69, 60

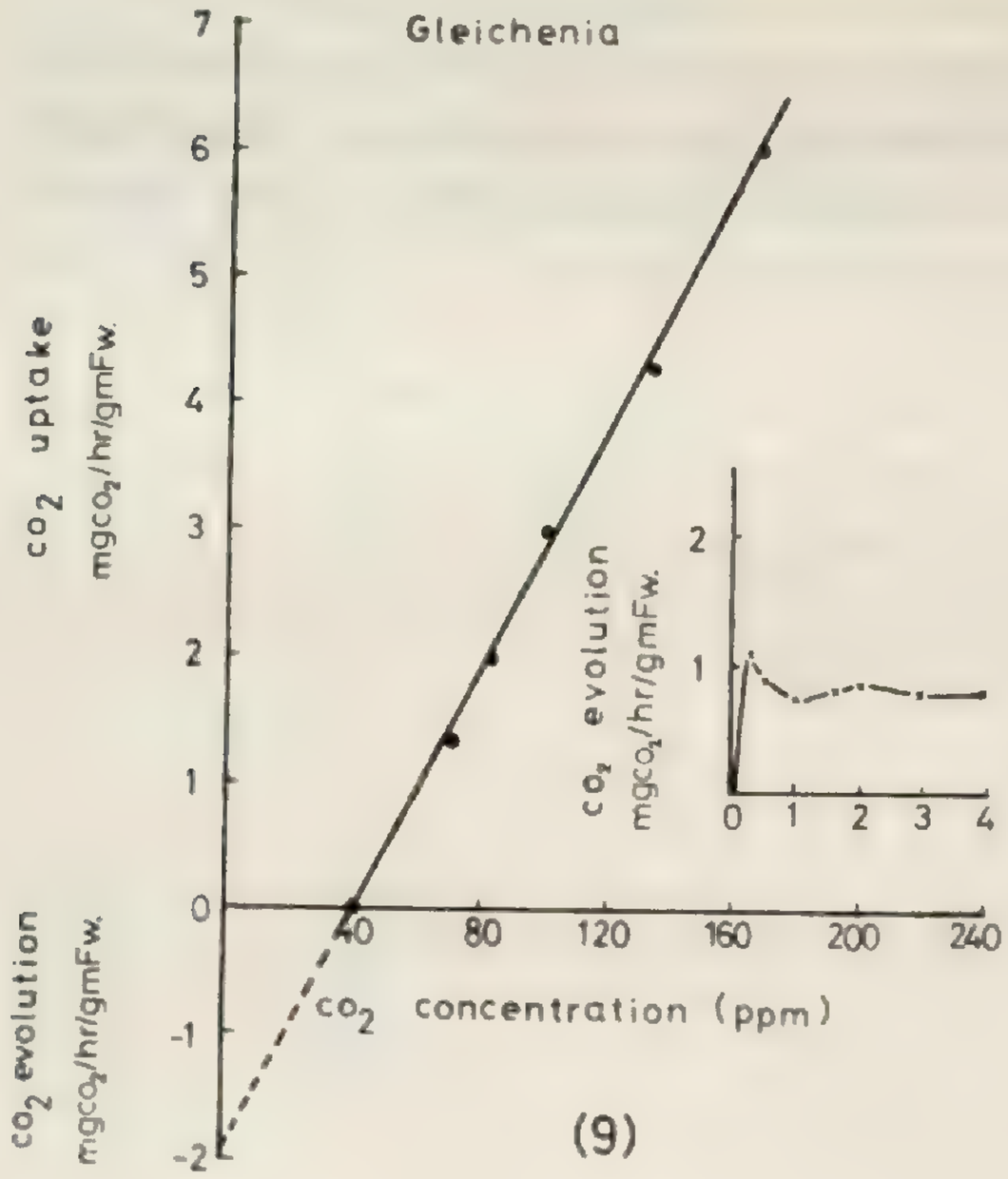
[1]Two replicates.

CRASSULEAN ACID METABOLISM

The fact that *Drymoglossum* showed no CO_2 uptake in light has led us to study the diurnal changes of its CO_2 fixation. Using a special, slow speed recorder, the CO_2 fixation and evolution of *Drymoglossum* was followed over a period of 24 hours. The results obtained are shown in *Fig. 14*. There was considerable CO_2 fixation in the dark, but little or no CO_2 fixation in the light. Instead, there was CO_2 evolution during the initial period of illumination.

DISCUSSION

The present investigation shows that the terrestrial sun ferns *Gleichenia* and *Nephrolepis* have high rates of apparent photosynthesis and saturate at a light intensity of 1×10^5 erg cm $^{-2}$ sec $^{-1}$. Apparent photosynthetic rates of shade-loving ferns, such as *Asplenium* and *Angiopteris*, were only one-sixth of that in sun ferns, and saturated at a very low light intensity. These results agree with the finding of sun and shade species of higher plants reported previously (Rabinowitch, 1951).



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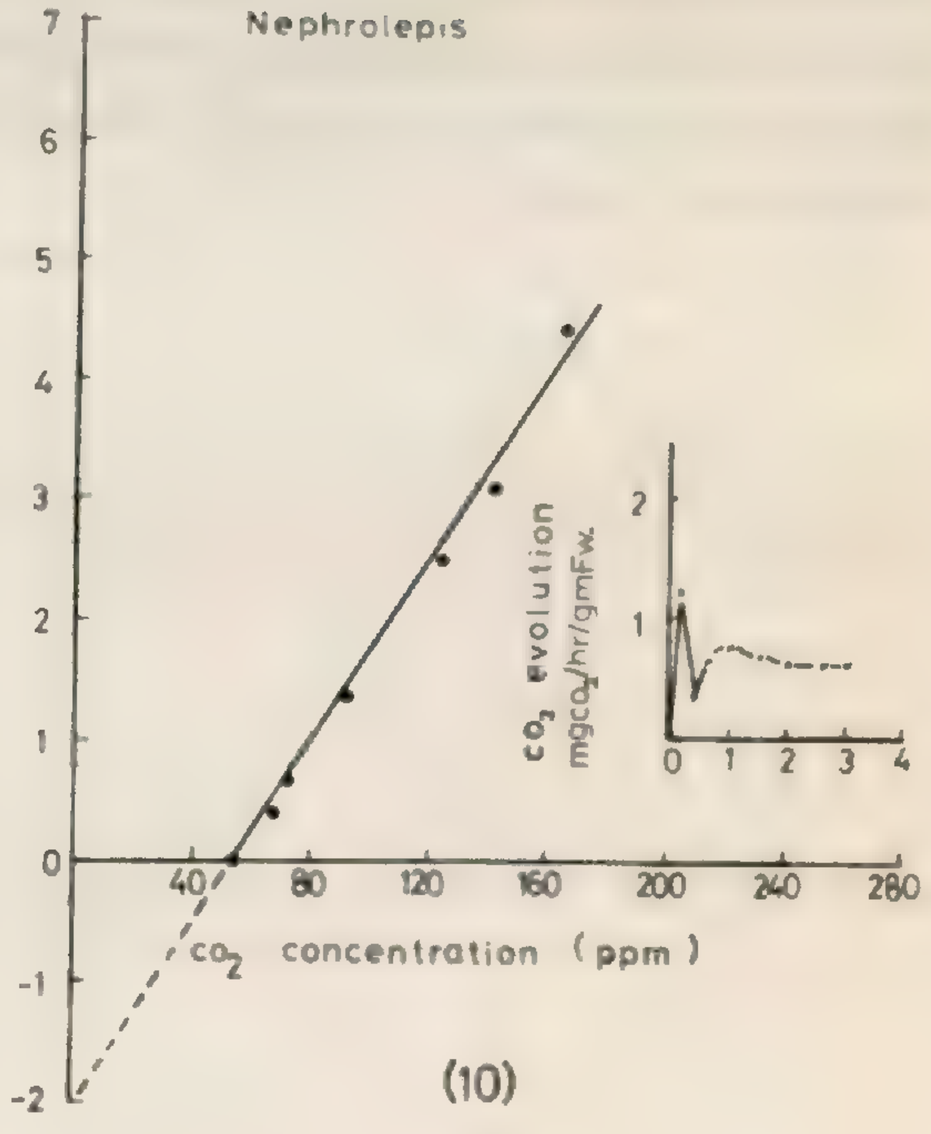

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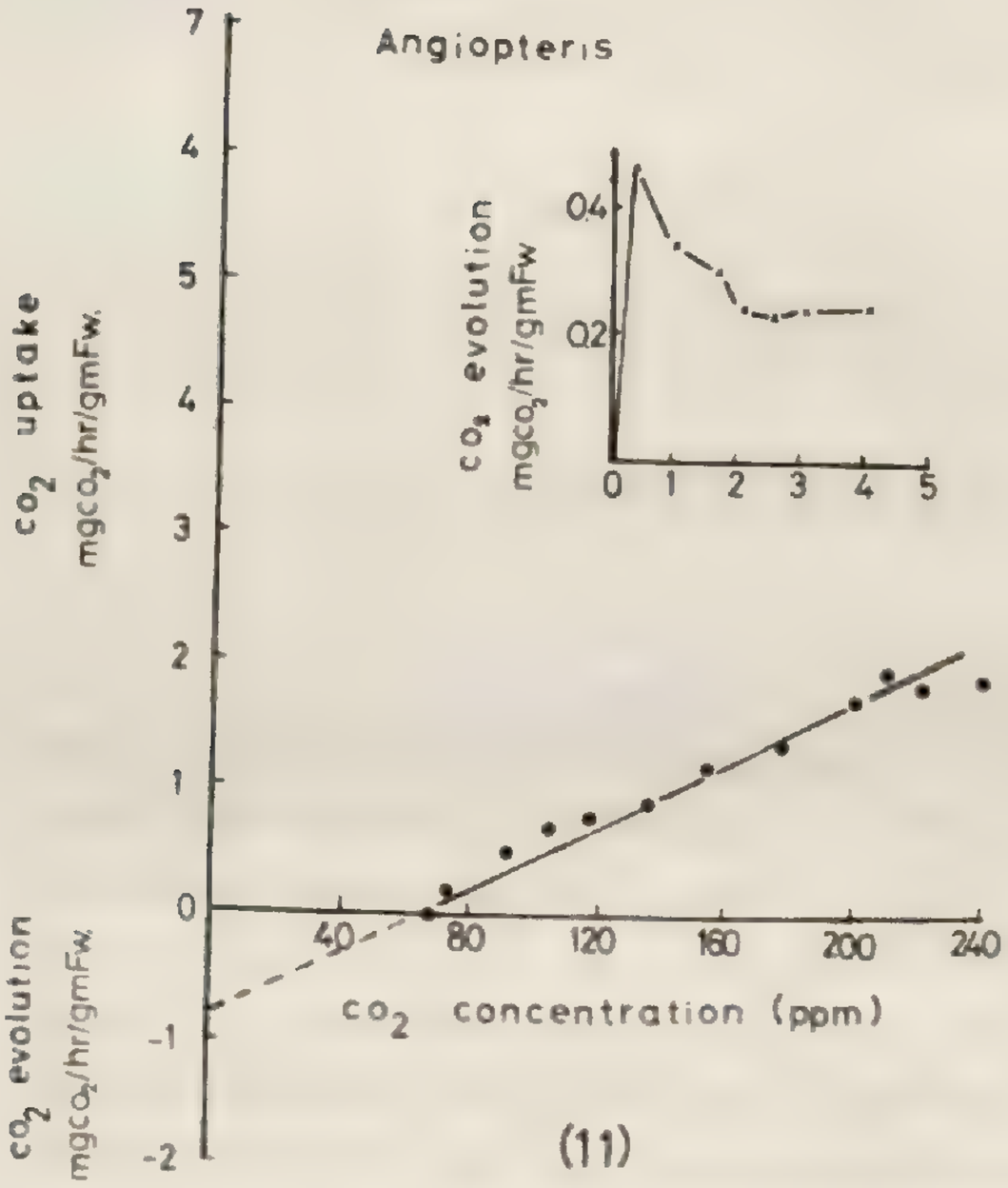

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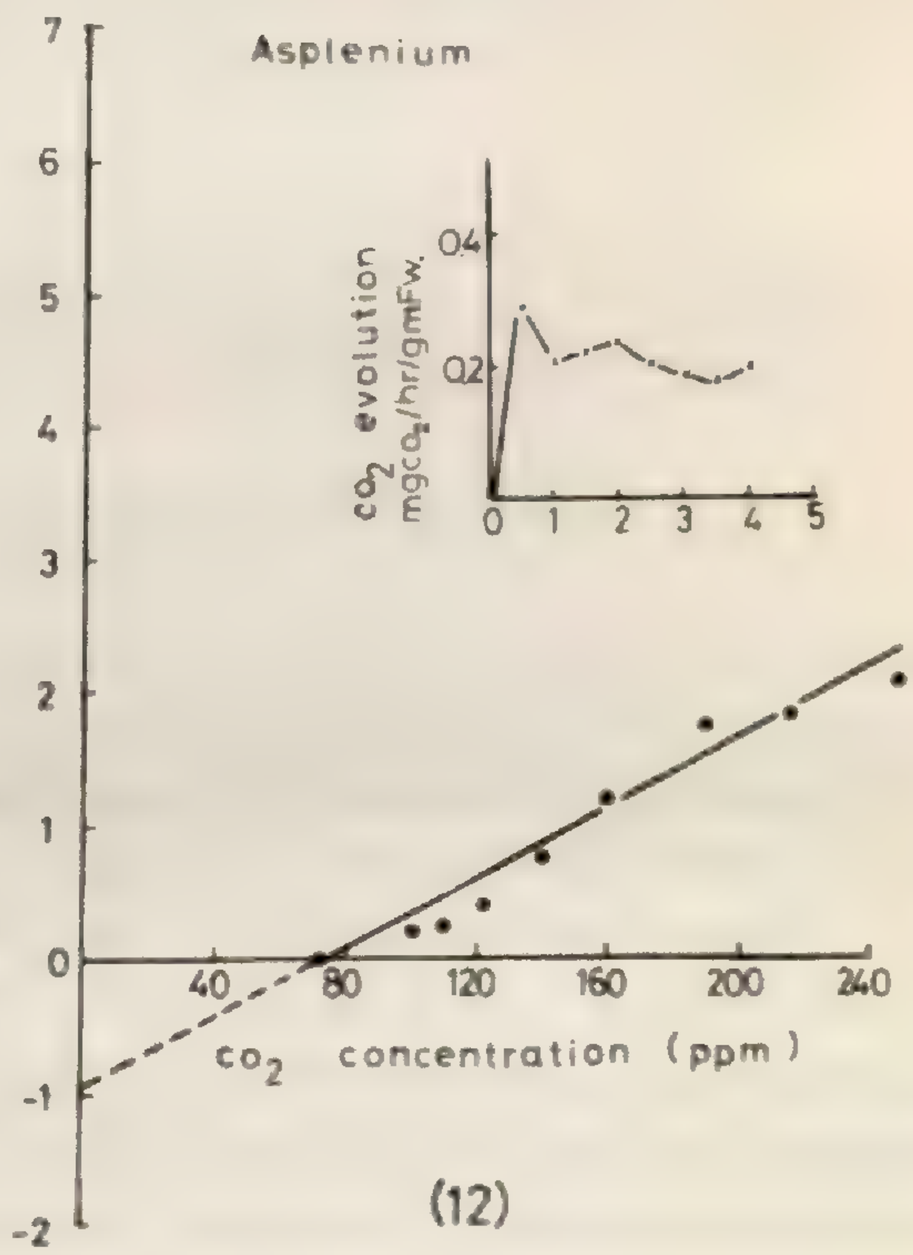

(12)

The effect of CO_2 concentration on apparent photosynthesis. FIG. 9. *Gleichenia*. FIG. 10. *Nephrolepis*. FIG. 11. *Angiopteris*. FIG. 12. *Asplenium*.

Because plants occurring in sunny habitats have considerably higher ribulose 1-5-diphosphate carboxylase activity than that of shade-loving plants, it has been concluded that low carboxylase activity in shade plants probably is one of the factors that limits the capacity for light-saturated photosynthesis in shade plants (Björkman, 1968).

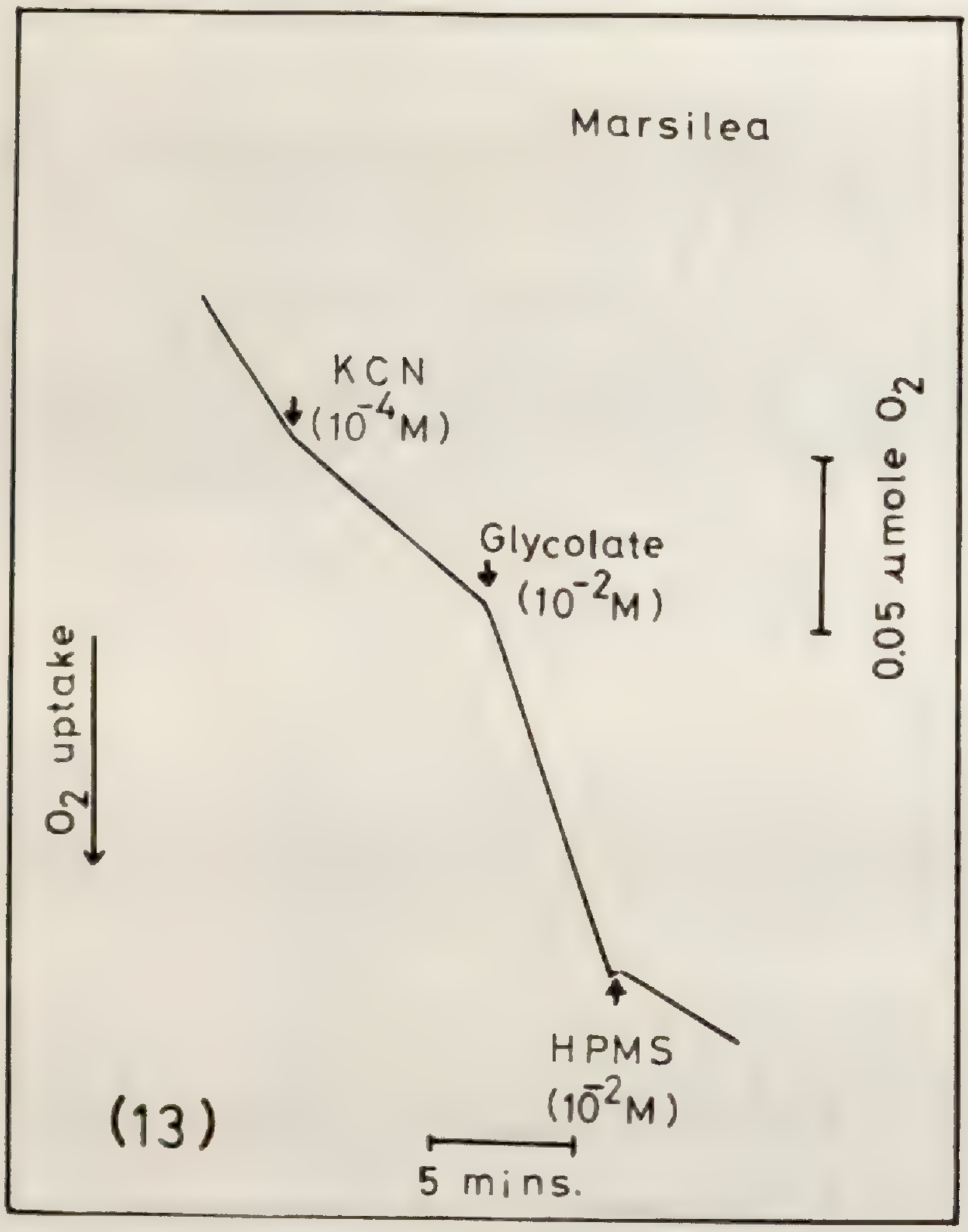

FIG. 13. A tracing of O_2 uptake by glycolic acid oxidase.

According to their mode of carbon fixation, higher plants have recently been divided into three groups: (1) the C_3 or Calvin cycle plants, (2) the C_4 or Hatch and Slack Pathway plants, and (3) plants which exhibit crassulean acid metabolism (Hatch & Slack, 1970). The first two groups fix CO_2 in the light and the latter fixes CO_2 in the dark. Based on δ 13 C value (Troughton, 1971) and taxonomic distribution (Evans, 1971), it has been suggested that the Calvin cycle is a more primitive pathway of photosynthesis, and that the CAM and C_4 pathways are recent addenda to the Calvin cycle. All plants, however, rely on the Calvin cycle for the ultimate step in CO_2 fixation; the CAM and C_4 pathways operate essentially as mechanisms for prefixing and concentrating CO_2 (Evans, 1971).

In our present investigation, all the ferns studied except *Drymoglossum* show prominent postillumination CO_2 outbursts; high CO_2 compensation points, and high photorespiratory rates; all these are typical characteristics of Calvin cycle plants (Jackson & Volk, 1970). It is interesting to note that *Angiopteris,* a primitive fern that is commonly regarded as a living fossil (Holttum, 1954), has photosynthetic characteristics very similar to a more modern fern like *Gleichenia*. The operation of the Calvin cycle in ferns is in agreement with the suggestion that the Calvin cycle is a primitive pathway of CO_2 fixation in the plant kingdom.

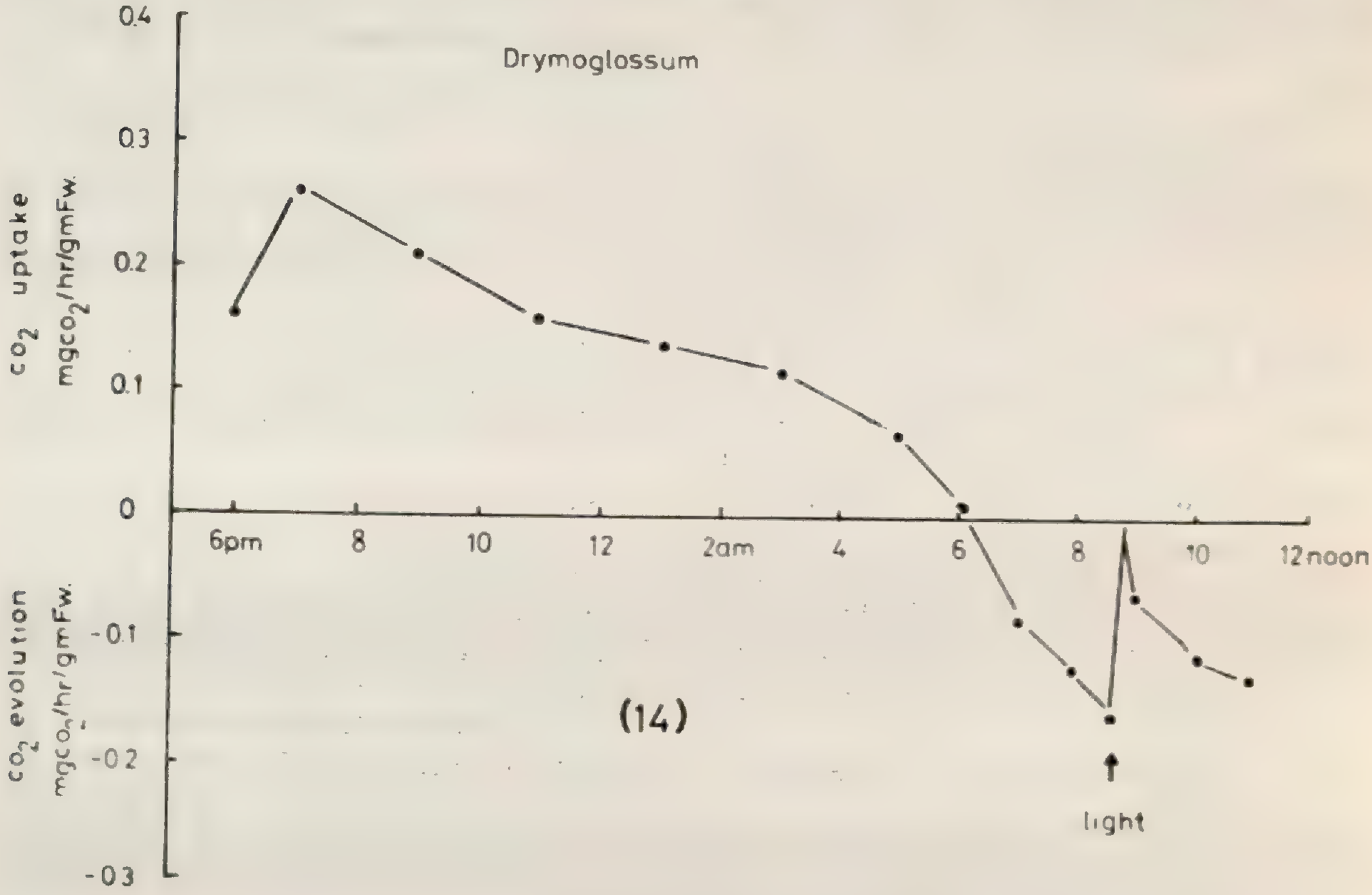

FIG. 14. Diurnal change of CO_2 gas exchange in *Drymoglossum*.

While all ferns studied fix CO_2 via the Calvin cycle, *Drymoglossum* exhibits non-autotropic CO_2 fixation. Recently, it has been demonstrated that crassulean acid metabolism is positively associated with succulent habit (McWilliams, 1970). It is generally believed that CAM is an adaptation to a xeric environment. Epiphytic habitats in tropical rain forests may be extremely xeric, indeed (Richards, 1952). However, it should be pointed out that although the epiphytic habitat may be xeric, it does not necessarily follow that an epiphyte would exhibit Crassulean acid metabolism. The difference in CO_2 fixation patterns between the two epiphytic ferns *Asplenium* and *Drymoglossum* is, therefore, worth noting. *Drymoglossum* fronds are succulent but *Asplenium* is not. Presumably, *Asplenium* is not under a strong xeric stress. This is probably attributed to the elaborate root system of *Asplenium,* which acts as a trap in retaining water and other organic materials (Holttum, 1957).

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Taxonomic Revision of the Polypodiaceous Genera of India–VI. Lepisorus excavatus Group[1]

S. S. BIR and CHANDER K. TRIKHA*

In an earlier paper Bir and Trikha (1972) treated 13 species of the *Polypodium lineare* complex in the Himalayas, one of which was *Lepisorus excavatus* (Bory) Ching. Further examination of herbarium material obtained from the Central National Herbarium, Howrah, India, and the U. S. National Herbarium, Washington, has shown that there are a few more species in the Himalayas belonging to the *L. excavatus* complex.

Taxonomically, *Lepisorus* (J. Smith) Ching is a most confusing and difficult genus because of the great similarity of its species and their variation (hybridization occurs between some of the species, especially those of the *L. excavatus* and *L. kashyapii* complexes).

The systematic position of *Lepisorus* is itself controversial. It has been recognized as a distinct genus (Christensen, 1938, p. 547; Ching, 1940, p. 258; Nayar, 1961; Holttum, 1968, p. 151; Bir & Trikha, 1968a, 1972) or merged with *Pleopeltis* (Copeland, 1947, p. 183; Panigrahi & Patnaik, 1965). Furthermore, *Lepisorus* (and also *Pleopeltis*) have similarities with *Microsorium* (Bir & Trikha, 1968b). Some species of the genus also have a superficial resemblance to *Phymatodes* because of the similar fronds and soral arrangement, but *Phymatodes* can be distinguished by its hair-like, club-shaped, elongate paraphyses and by the prominent lateral veins of its laminae. Holttum (1968, p. 151) separated *Lepisorus* from other polypodiaceous genera and mentioned the characteristic umbrella-shaped paraphyses which protect the sporangia, especially in young stages. Although the under surface of the laminae of some of the taxa described here is covered with scales, these scales are different from those of *Pleopeltis*, like *P. macrocarpa* (Bory ex Willd.) Kaulf. In *Lepisorus* the laminar scales are absent or deciduous, but in *Pleopeltis* they are persistent. Furthermore, the rhizome scales in *Lepisorus* are attached towards the base, but in *Pleopeltis* they are centrally attached. The distinction between these two genera does not appear to be very sharp. But for the very close resemblance in external morphology and scale structure of the scaly *Lepisorus* species (e. g., *L. oligolepidus*, *L. suboligolepidus*, *L. excavatus* var. *himalayensis* and var. *mortonianus*, and *L. amaurolepidus* var. *longifolius*) with the non-scaly ones, the scaly species could have easily been included in *Pleopeltis*.

As a consequence of our cytotaxonomic studies on the Himalayan members of *Lepisorus*, we discovered several new taxa. All the species treated resemble each other very closely and are sympatric. The chief diagnostic characters are in the rhizome scales and spores. The total number of fully described and illustrated

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[1] We wish to express our grateful thanks to the Directors or Keepers of the cited herbaria for lending us valuable material for study, and to the late C. V. Morton and to D. B. Lellinger for valuable suggestions on taxonomical and nomenclatural matters.

Lepisorus species in India is now 20 (see also Bir & Trikha, 1972; Bir & Shukla, 1971). In addition, three taxa of *Pleopeltis* have been described for India (Bir & Trikha, 1968a).

KEY TO THE SPECIES OF LEPISORUS

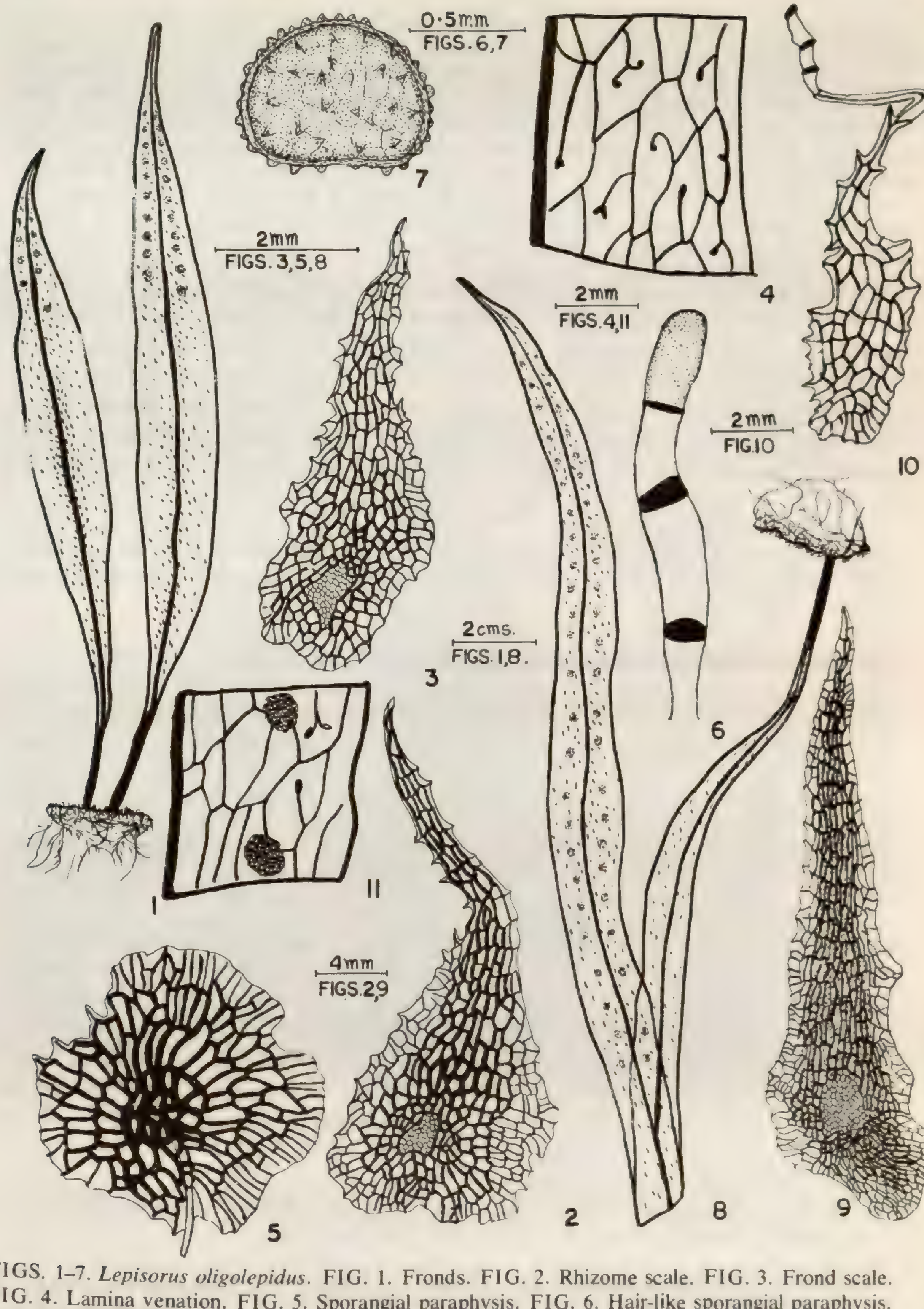
1. Rhizomes more than 5 mm in diam.
   2. Rhizome scales with large, clear, isodiametric lumina, concolorous.
      3. Laminae coriaceous, the venation hidden; sori nearer to the midrib than the margin; spores tuberculate ..... 1. *L. oligolepidus*
      3. Laminae chartaceous or subcoriaceous, the venation apparent; sori medial; spores verrucose. 2. *L. suboligolepidus*
   2. Rhizome scales with large, clear, isodiametric lumina, concolorous.
      4. Laminae broadly ovate-lanceolate, broadest in the lower third, chartaceous or coriaceous; sori not sunken; spores verrucose ..... 3. *L. sublinearis*
      4. Laminae lanceolate or narrowly ovate-lanceolate, broadest in the middle, papyraceous, membranaceous, or subcoriaceous; sori deeply sunken; spores tuberculate or verrucose.
         5. Laminae broadly lanceolate with an acute apex, 4–5 cm wide, subcoriacous, yellowish-brown when dry ..... 6. *L. oosphaerus*
         5. Laminae lanceolate or narrowly ovate-lanceolate, 2–4 cm wide, not subcoriaceous, not yellowish-brown when dry.
            6. Laminae lanceolate with an acuminate apex, 2–2.5 cm wide, papyraceous, blackish-brown when dry ..... 4. *L. leiopteris*
            6. Laminae narrowly ovate-lanceolate with an acute apex, 2–4 cm wide, membranaceous, pale greenish when dry.
               7. Rhizome scales serrate-dentate; sporangial paraphyses either 1- or 2-celled or stellate with protruding teeth ..... 5c. *L. excavatus* var. *himalayensis*
               7. Rhizome scales erose or nearly entire; sporangial paraphyses all umbrella-shaped with an entire margin.
                  8. Rhizome scale cells uniformly thickened; spores tuberculate. 5a. *L. excavatus* var. *excavatus*
                  8. Rhizome scale cells thin-walled at the margin and thick-walled at the center; spores verrucose to tuberculate-granulate ..... 5b. *L. excavatus* var. *mortonianus*
1. Rhizome up to 3 mm in diam.
   9. Rhizome scales concolorous, sparingly toothed ..... 7. *L. sordidus*
   9. Rhizome scales bicolorous, prominently toothed.
      10. Stipes 2–4 mm distant, 0.5–1 cm long; laminae 4–8 mm wide, linear; sori submedial, confluent toward the lamina apex ..... 8. *L. subconfluens*
      10. Stipes 5–10 mm distant, 1–3 cm long; laminae 5–20 mm wide, linear-lanceolate; sori medial, not confluent towards the lamina apex.
         11. Fronds 6–25 cm long; laminae beneath almost glabrous except for a few scales at the midrib; young paraphyses without marginal glandular cells. 9a. *L. amaurolepidus* var. *amaurolepidus*
         11. Fronds more than 25 cm long; laminae beneath entirely covered with deciduous scales with glandular apical cells; young paraphyses with marginal glandular cells. 9b. *L. amaurolepidus* var. *longifolius*

1. Lepisorus oligolepidus (Baker) Ching, Bull. Fan Mem. Inst. Biol. 4: 80. 1933.

Figs. 1–7.

Polypodium oligolepidum Baker, Gard. Chron. n.s., **14**: 494. 1880.
Polypodium lineare var. *oligolepidum* (Baker) Christ, Bull. Soc. Bot. France **52**, Mém. **1**: 15. 1905.

Rhizome 5–8 mm in diam., densely scaly, the scales 5–8 mm long, 0.5–0.7 mm wide, narrowly ovate-lanceolate to subulate with a broad base, rigid, bicolorous,



FIGS. 1–7. *Lepisorus oligolepidus*. FIG. 1. Fronds. FIG. 2. Rhizome scale. FIG. 3. Frond scale. FIG. 4. Lamina venation. FIG. 5. Sporangial paraphysis. FIG. 6. Hair-like sporangial paraphysis. FIG. 7. Spore. FIGS. 8–11. *L. suboligolepidus*. FIG. 8. Frond. FIG. 9. Rhizome scale. FIG. 10. Frond scale. FIG. 11. Lamina venation.

opaque in the center, the margin with protruding teeth; stipes 0.5–2 cm long, woody; laminae 15–21 cm long, 1–2 cm broad, lanceolate with an acuminate apex, obscurely black when dry, coriaceous, the venation hidden, the surface beneath covered with deciduous, black, ovate-lanceolate, long-acuminate scales with protruding marginal teeth, the surface above glabrous and often punctate; sori usually 4–5 mm in diam., round, closer to the midrib than the margin; sporangial paraphyses circular, thick in the center, reddish- to blackish-brown, 2–many-celled, hair-like paraphyses with a glandular apical cell also present; annulus 14–16-celled; spores light yellow, tuberculate, granulate, oval or plano-convex to concavo-convex, 55–80 × 46–63 μm.

DISTRIBUTION: Himalayas, Burma, China, and Japan.

This species is very rare in India, collected only once in Mussoorie. It matches exactly a Burmese specimen, *Rock 7494* (US 1211846), identified as *P. oligolepidum* Baker by Christensen. Mitui (1971) has described the morphology of *L. oligolepidus* and has placed it in the opaque group, in which the rhizome scales are bicolorous with a blackish-brown midrib and a transparent margin and the sporangial paraphyses are circular. He describes six species in the group, all having $x = 25$ or 26.

SPECIMENS EXAMINED:

INDIA: Uttar Pradesh: Mussoorie, Aruigadh stream in South East, 1500 m, Feb 1903, *Mackinnon* (CAL). **BURMA:** Between Sadon and the Yunnan, China border at Chaugtifang and Kambaiti, Nov 1922, *Rock 7494* (US).

2. Lepisorus suboligolepidus Ching, Bull. Fan Mem. Inst. Biol. 4: 77. 1933.

Figs. 8–13.

Polypodium neurodioides form 2. C. Chr. Contr. U. S. Nat. Herb. **26**: 319. 1931, *nom. illeg.*

Rhizome wide-creeping, 5–6 mm in diam., densely scaly, the scales 4–9 mm long, ca. 0.05 mm wide, narrowly ovate-lanceolate, acuminate, bicolorous, opaque in the center, dark brown, the margin erose, the marginal and basal cells hyaline with clear, elongate lumina and thin walls; stipes 2–4 cm long, at least 1.5 cm distant, stramineous; laminae 16–28 cm long, 1.5–2.5 cm wide, lanceolate, long-attenuate, broadest in the lower third, decurrent to the base, dull green when dry, rigid, chartaceous, or subcoriaceous, the venation distinct, scaly on the under surface, the scales lanceolate to broadly ovate-lanceolate with a long-acuminate apex and a glandular apical cell when young; sori 2–4 mm in diam., medial, confined to the upper part of the laminae; sporangial paraphyses circular, thick, dark brown; annulus 12–17-celled; spores hyaline to pale yellow, slightly verrucose, oval to reniform or concavo-convex, regular, 58–79 × 37–46 μm.

DISTRIBUTION: Himalayas and China.

This species is epiphytic or lithophytic in the Himalayas from Kashmir to Darjeeling and Sikkim, at 300–1500 m elevation, and is not common. It has long been confused with *L. excavatus*.

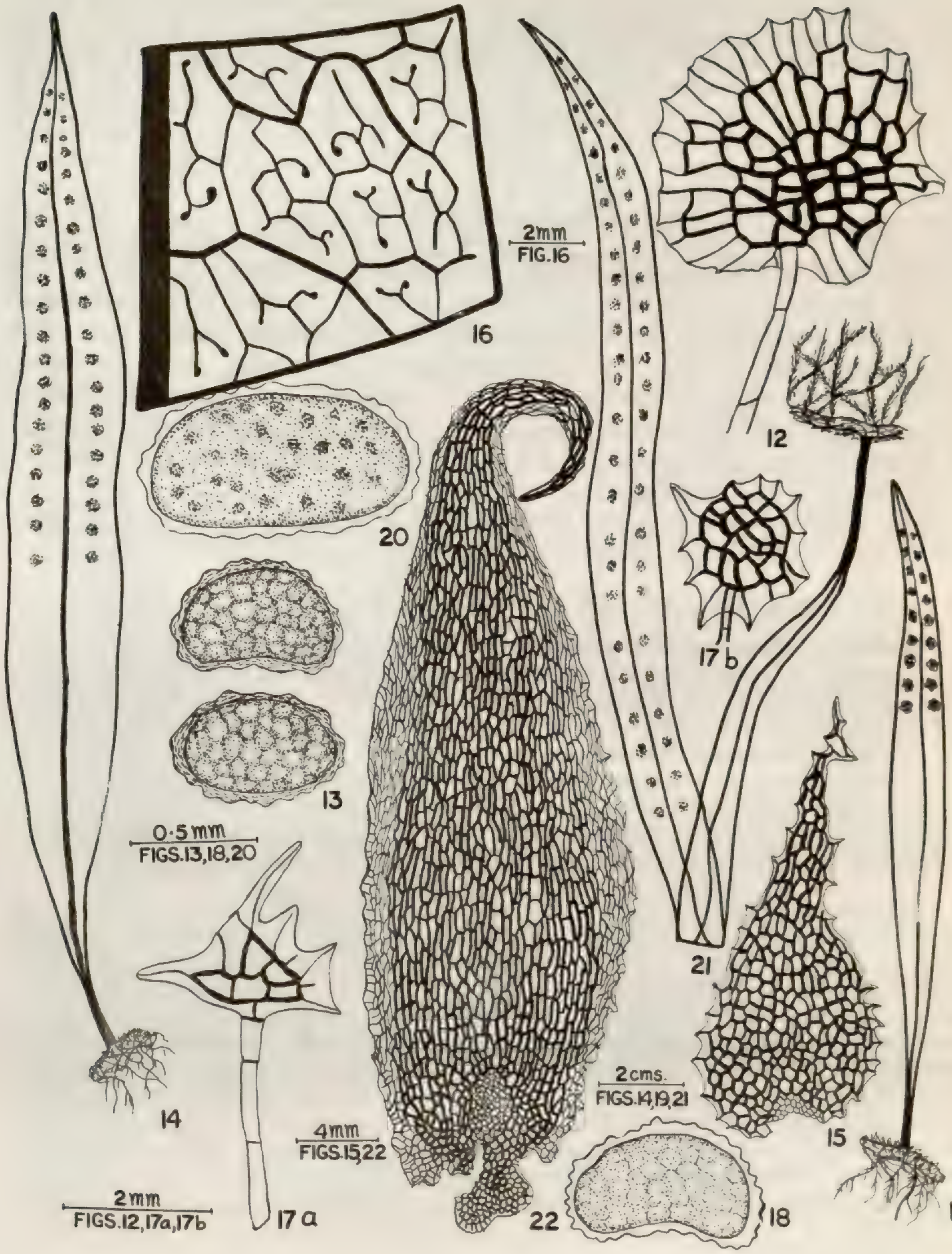
SPECIMENS EXAMINED:

INDIA: Kashmir: Sonamarg, 1050 m, Aug 1921, *Stewart* (US). **ASSAM:** Sept 1882, *Godfrey 273* (CAL). **SIKKIM:** Rangbee stream, 500 m, Sept 1887, *King 4005* (CAL).

3. Lepisorus sublinearis (Baker) Ching, Bull. Fan Mem. Inst. Biol. 4: 78. 1933.

Figs. 14–18.

Polypodium sublineare Baker ex Takeda, Notes Roy. Bot. Gard. Edinb. **8**: 276. 1915.



FIGS. 12–13. *Lepisorus suboligolepidus*. FIG. 12. Sporangial paraphysis. FIG. 13. Spore. FIGS. 14–18. *L. sublinearis*. FIG. 14. Frond. FIG. 15. Rhizome scale. FIG. 16. Lamina venation. FIGS. 17a, b. Sporangial paraphyses. FIG. 18. Spore. FIGS. 19–20. *L. sublinearis* × *sordidus*. FIG. 19. Frond. FIG. 20. Spore. FIGS. 21–22. *L. leiopteris*. FIG. 21. Frond. FIG. 22. Rhizome scale.

Rhizome creeping, hypogeous, at least 5 mm in diam., densely scaly, the scales 3–5 mm long, 5 mm wide, ovate-lanceolate, concolorous, fuscous, coarsely clathrate, with large, clear, almost isodiametrical lumina, the margin with short, stout, protruding teeth; stipes 0.5–1 cm distant, 2.5–8 cm long, stramineous; laminae 22–35 cm long, 2–2.7 cm wide, broadly ovate-lanceolate, broadest in the lower third, attenuate to the apex, the margin plane, brown when dry, thick, chartaceous or subcoriaceous, the venation obscure; sori 2–3 mm in diam., round, nearer the margin than the midrib, in the apical half of the laminae; sporangial paraphyses stellate to umbrella-shaped; annulus 13–16-celled; spores yellow, verrucose, oval to round or plano- to concavo-convex, 50–75 × 37–50 μm.

DISTRIBUTION: Eastern Himalayas, Burma, and China.

This species is an epiphyte in the forests of Assam at 1200–1800 m elevation and is not very common. Some epiphytic specimens from the Duphia Hills, 2040 m altitude (*Lister* in 1874, CAL) are intermediate between *L. sordidus* and *L. sublinearis*. They have scales like those of *L. sublinearis* and fronds like those of *L. sordidus*. They have minutely verrucose spores of irregular size (*Figs. 19–20*). It is possible that these specimens are hybrids between these two species.

SPECIMENS EXAMINED:

INDIA: Assam: Manipur, 1800 m, April 1882 *Watt* (CAL), 600 m, April 1882, *Watt* (CAL); Kohima, 400 m, April 1896, *King* (CAL). **BURMA:** Nov 1922, *Rock 7424* and *7509* (both US).

4. Lepisorus leiopteris (Kunze) Bir & Trikha, comb. nov. Figs. 21–26.

Polypodium scolopendrium Buch.-Ham. ex D. Don, Prodr. Fl. Nepal. 1. 1825, *nom. illeg., non P. scolopendria* Burm., 1768. The two names are orthographic variants, and so Don's name is a later homonym, according to C. V. Morton (*in litt.*).

Polypodium leiopteris Kunze, Linnaea **23:** 279, 319. 1850. According to Ching (1933, p. 69), this is the earliest available name for this species.

Lepisorus excavatus var. *scolopendrium* (D. Don) Ching, Bull. Fan Mem. Inst. Biol. **4:** 69. 1933.

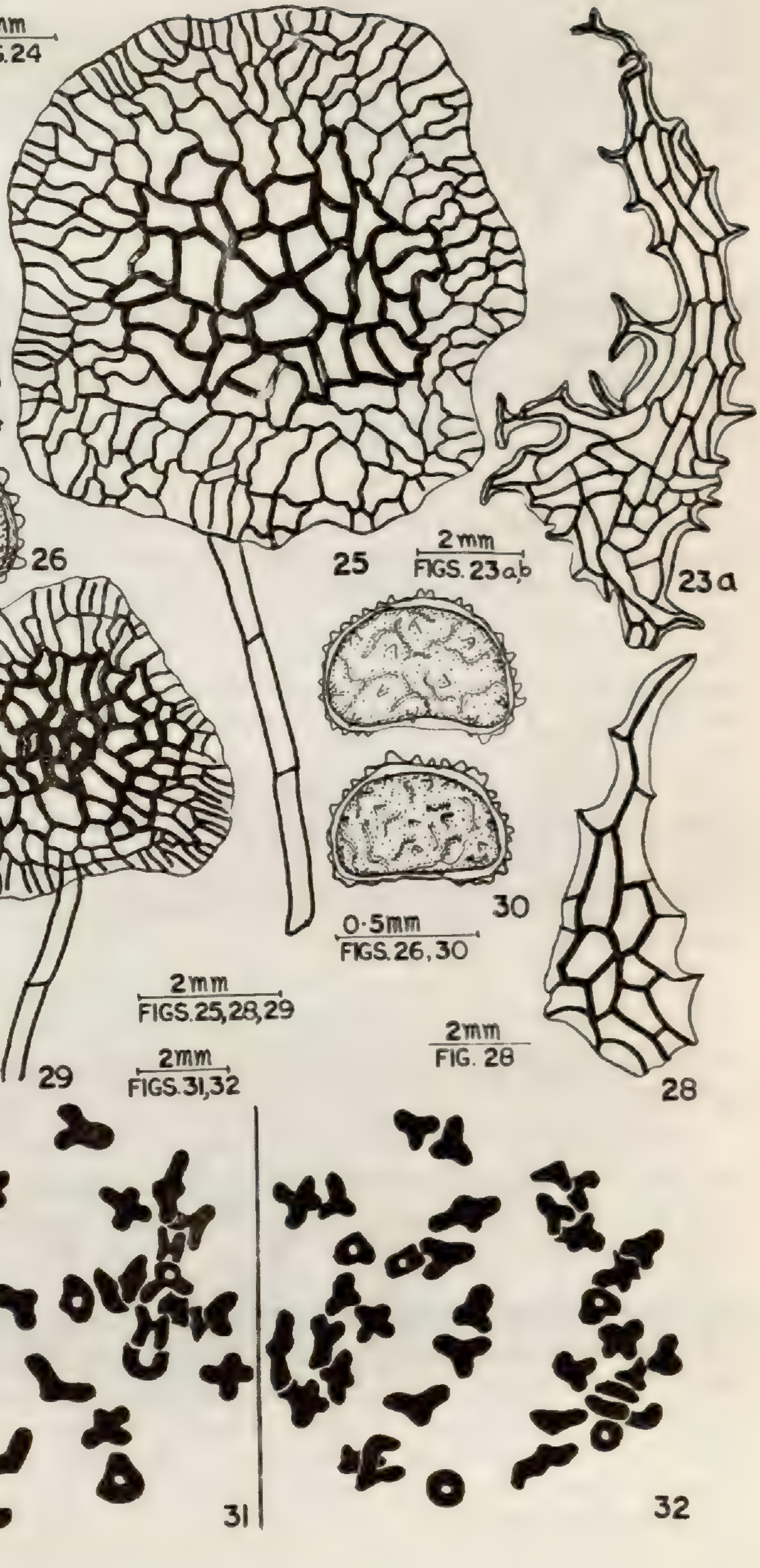
Pleopeltis scolopendrium (D. Don) Alston & Bonner, Candollea **15:** 207. 1956.

Lepisorus scolopendrium (D. Don) Mehra & Bir, Res. Bull. Panjab Univ. Sci. n.s., **15:** 168. 1964, as "*scolopendrius*." The old, indeclinable generic name ought not to have been altered.

Rhizome wide-creeping, 5–6 mm in diam., superficial, with a tuft of wiry roots, densely scaly, the scales 3–8 mm long, 1–1.5 mm wide, broadly ovate-lanceolate with an acuminate apex, concolorous, brown, clathrate, the central cells thick-walled and brown, the margins erose, the marginal cells thin-walled and yellow; stipes 0.5–5 cm long, stramineous; laminae 30–40 cm long, 2–2.5 cm wide, lanceolate with a long-acuminate apex, the margin wavy, attenuate to the base, blackish-brown when dry, scaly beneath, the scales deciduous and glandular when young, papyraceous with prominent veins, the venation distinct, the main veins quite prominent; sori 3–5 mm in diam., nearer the midrib than the margin, deeply sunken and forming prominent pustules on the upper surface; sporangial paraphyses umbrella-shaped, clathrate, peltate, thin, pale yellow; spores more or less tuberculate, round to oval or elliptical, concavo- to plano-convex, 63–75 × 37–55 μm.

DISTRIBUTION: Himalayas.

This is one of the commonest species of the genus at 1500–2700 m altitude in the eastern Himalayas, and is either epiphytic or lithophytic. The rhizome apex often projects away from the substrate and is borne on a tuft of wiry roots.



FIGS. 23–26. *Lepisorus leiopteris*. FIGS. 23a, b. Frond scales. FIG. 24. Lamina venation. FIG. 25. Sporangial paraphysis. FIG. 26. Spore. FIGS. 27–32. *L. excavatus* var. *mortonianus*. FIG. 27. Rhizome scale. FIG. 28. Frond scale. FIG. 29. Sporangial paraphysis. FIG. 30. Spore. FIGS. 31–32. Spore mother cell at metaphase-I showing 37 bivalent chromosomes.

SPECIMENS EXAMINED:

INDIA: Darjeeling: Peshok, Aug 1862, *Anderson* (CAL), 600–900 m, Aug 1862, *Anderson* (CAL), *Anderson 1472* (CAL); Senchal, 2400 m, July 1880, *Gamble 8212* (CAL), 2500 m, June 1900, *Levinge* (CAL); Tonglu, Aug-Sept 1887, *King's collector* (CAL), *Mehra 12* (US). **ASSAM:** Kula Kawa, July 1882, *Godfrey 253* (CAL); Khasya, 1200–2100 m, *Hooker & Thomson* (US), July 1850, *Hooker & Thomson* (CAL); Khasya Hills, 1500 m, Aug 1889, *Mann* (US); Naga Hills, 1800–2100 m, Aug 1862, *Prain* (CAL). **SIKKIM:** July 1887, *Wallich* (CAL), *Devi* (CAL), Oct 1887, *Hooker* (CAL); Phedoucher, 2400 m, July 1880, *Gamble* (CAL), 2400 m, Aug 1910, *Smith 4399* (CAL); Choongthung, 1950 m, May 1886, *King* (CAL).

5a. Lepisorus excavatus (Bory) Ching, Bull. Fan Mem. Inst. Biol. 4: 68. 1933, var. exavatus[2]

Polypodium excavatum Bory ex Willd. Sp. Pl. ed. 4, **5:** 158. 1810.
Polypodium lineare Clarke, Trans. Linn. Soc. London II, Bot. **1:** 558. 1880, *pro parte*.
Polypodium simplex Bedd. Handb. Ferns Brit. India 347. 1883.
Pleopeltis excavata Sledge, Bull. Brit. Mus. Nat. Hist. **2**(5): 138. 1960.

Rhizome wide-creeping, 4–9 mm in diam., compressed, woody in some specimens, scaly, the scales lanceolate, 3–7 mm long, 1–1.5 mm wide, acuminate, dull brown, clathrate with a slightly erose margin; fronds 1–2 cm distant; stipes 0.5–4 cm long, yellowish-green; laminae 14–42 cm long, 2–4 cm wide, ovate-lanceolate, decurrent at the base, the apex acute, pale or greenish when dry, stiff, membranaceous, the venation prominent, scaly on the under surface along the midrib, the scales thick in the center, yellowish-brown, deciduous; sori 3–5 mm in diam., nearer the midrib than the margin, deeply sunk forming pustules on the upper side of the laminae; sporangial paraphyses thick in the center, with a rather short stalk; spores light brown, more or less tuberculate, oval to reniform, 48–69 × 34–45 μm.

DISTRIBUTION: Himalayas, South India, Japan, tropical Africa and Madagascar.

This species is frequent in the Himalayas and usually is an epiphyte at 1500–2100 m elevation, but is comparatively rare in the Eastern Himalayas towards Darjeeling. It is also found in the mountains of South India at comparable altitudes.

The following two new varieties are cytologically distinct, and are reported for the first time. They have $n = 37$ and $n = 36$, respectively, in contrast to $n = 35$ for var. *excavatus* (Malhotra in Mehra, 1961; Panigrahi & Patnaik, 1961; Bir & Trikha, unpubl.).

5b. Lepisorus excavatus var. mortonianus Bir & Trikha, var. nov. Figs. 27–32.

Paleae rhizomatis late ovato-lanceolatae, apice longe acuminatae, medio paullo crassae, bicolores, margine erosae; frondae paullo approximatae, breviter stipitatae, stipite ca. 15 mm longo; laminae subtus cum paleis eis var. *himalayensis* similibus; paraphyses sororum monomorphae, circulares, umbraculiformes, bicolores; sporae verrucosae vel tuberculatae, granulosae, 63–67 × 42–46 μm; $n = 37$.

TYPE: Near Tiffon top, Nainital, epiphytic, 2250 m, July 1971, *Trikha 1905* (PUN 1121;[3] isotypes PUN 1122, 1123, 1124).

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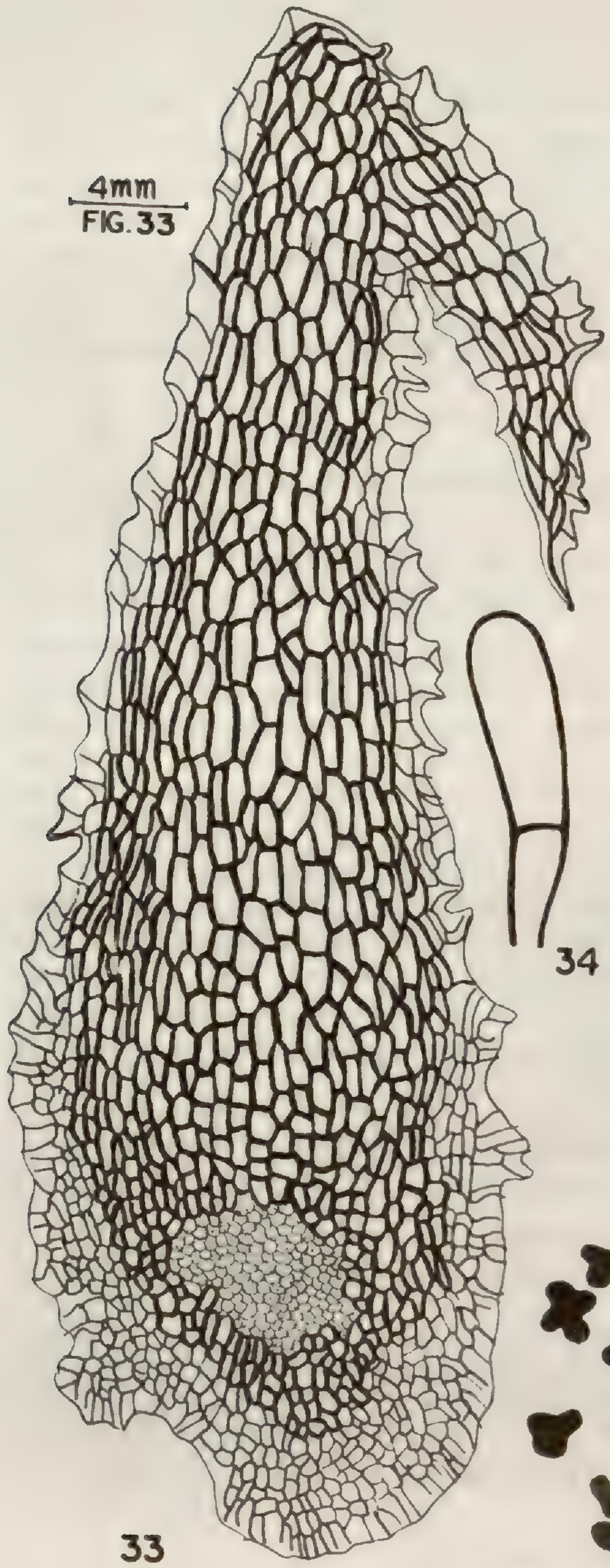
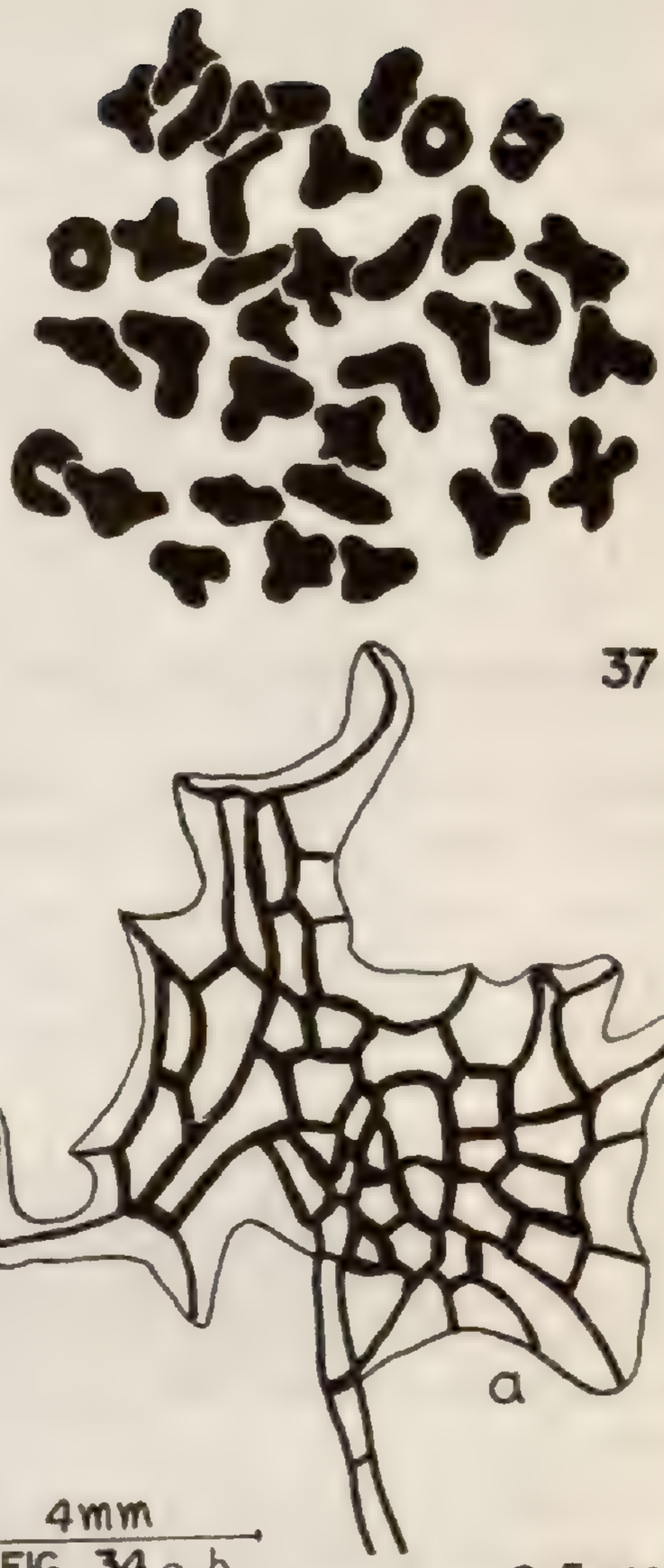
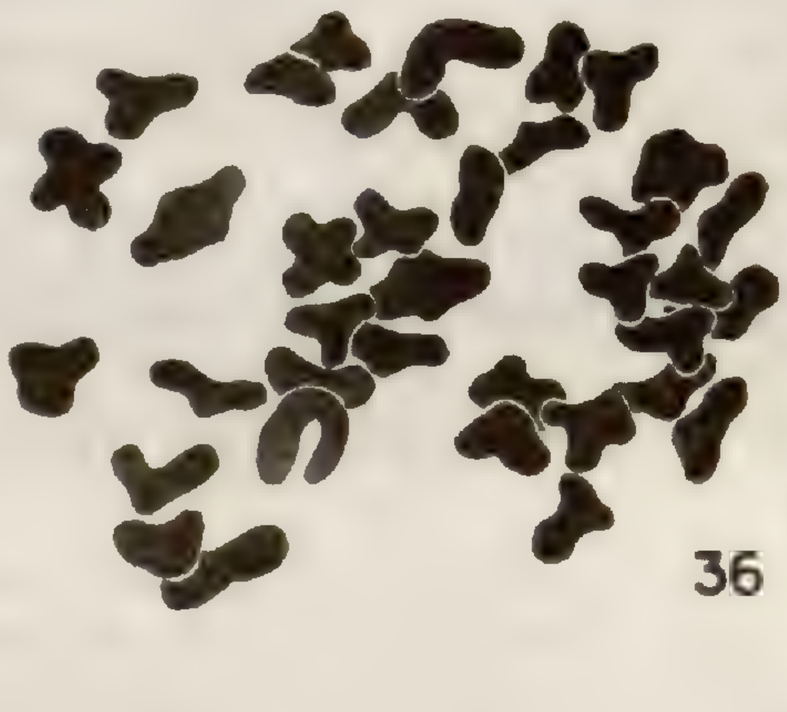
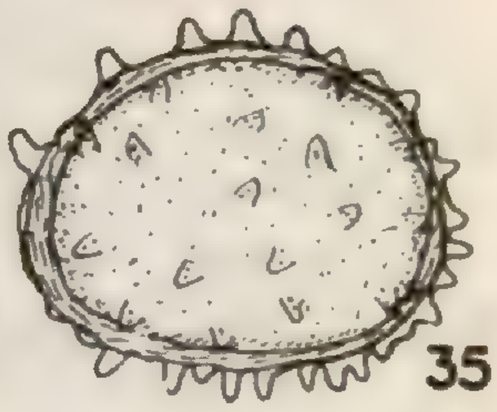
[2]For illustrations, see Bir and Trikha (1972, *f. 3, 46–49*).

[3]Abbreviation for the herbarium of Punjabi University, Patiala 147 002, India.









FIGS. 33–37. *Lepisorus excavatus* var. *himalayensis*. FIG. 33. Rhizome scale. FIGS. 34a, b. Sporangial paraphyses. FIG. 35. Spore. FIGS. 36–37. Spore mother cells at metaphase-I showing 36 bivalent chromosomes.

This variety is named in honor of the late C. V. Morton, who initiated the senior author's interest in fern taxonomy.

5c. Lepisorus excavatus var. himalayensis Bir & Trikha, var. nov. Figs. 33–37.

Paleae rhizomatis ovato-lanceolatae, saepe concolores, margine serrato-dentatae; laminae subtus parce paleaceae, paleis ovato-lanceolatis, longe acuminatis; paraphyses sororum dimorphae, nonnullae stellatae, brachiis elongatis patentibus, alterae simplices, piliformes, 1- vel 2-cellulares; sporae tuberculatae, 55–92 × 35–63 μm; $n = 36$.

TYPE: Nainital, Cheena Peak, not common, 2400 m, July 1971, *Trikha 1100* (PUN 1125; isotypes PUN 1126, 1127, 1128).

6. Lepisorus oosphaerus (C. Chr.) Ching, Bull. Fan Mem. Inst. Biol. 4: 70. 1933. Figs. 38–42.

Polypodium oosphaerum C. Chr. Contr. U. S. Nat. Herb. **26:** 334, *pl. 29.* 1931.
Pleopeltis oosphaera (C. Chr.) Panigrahi & Patnaik, Proc. Nat. Acad. Sci. India B, **34:** 482. 1964.

Rhizome wide-creeping, 5–8 mm in diam., clothed with long, wiry roots, densely scaly, the scales 2–8 mm long, 1–2.5 mm wide, lanceolate with an acuminate apex, concolorous, light brown, the lumina clear, narrow, the central cells thickened, the margin erose; fronds 2–3 cm distant; stipes up to 0.5 cm long; laminae 30–40 cm long, 4–5 cm wide, broadly lanceolate, widest below the middle, the apex acute, abruptly narrowed towards the decurrent base, yellowish-brown when dry, subcoriaceous, the venation conspicuous on the upper side, the lateral midveins not prominent, up to 6 areolae between the margin and the midrib; sori up to 5 × 8 mm, oblong, medial, slightly punctate on the upper surface, often confluent towards the apex; sporangial paraphyses peltate, clathrate, nearly smooth-margined and with a few middle cells highly thickened; annulus 12–15-celled; spores pale yellow to hyaline, tuberculate, oval to elliptic, plano- to concavo-convex, 59–76 × 37–55 μm.

DISTRIBUTION: Eastern Himalayas and northern Thailand.

This rare fern was reported from the Lushai Hills, Assam, in the eastern Himalayas by Fischer (1938). It has broad fronds and is distinct in the *L. excavatus* group because of its large, oblong, and often confluent sori.

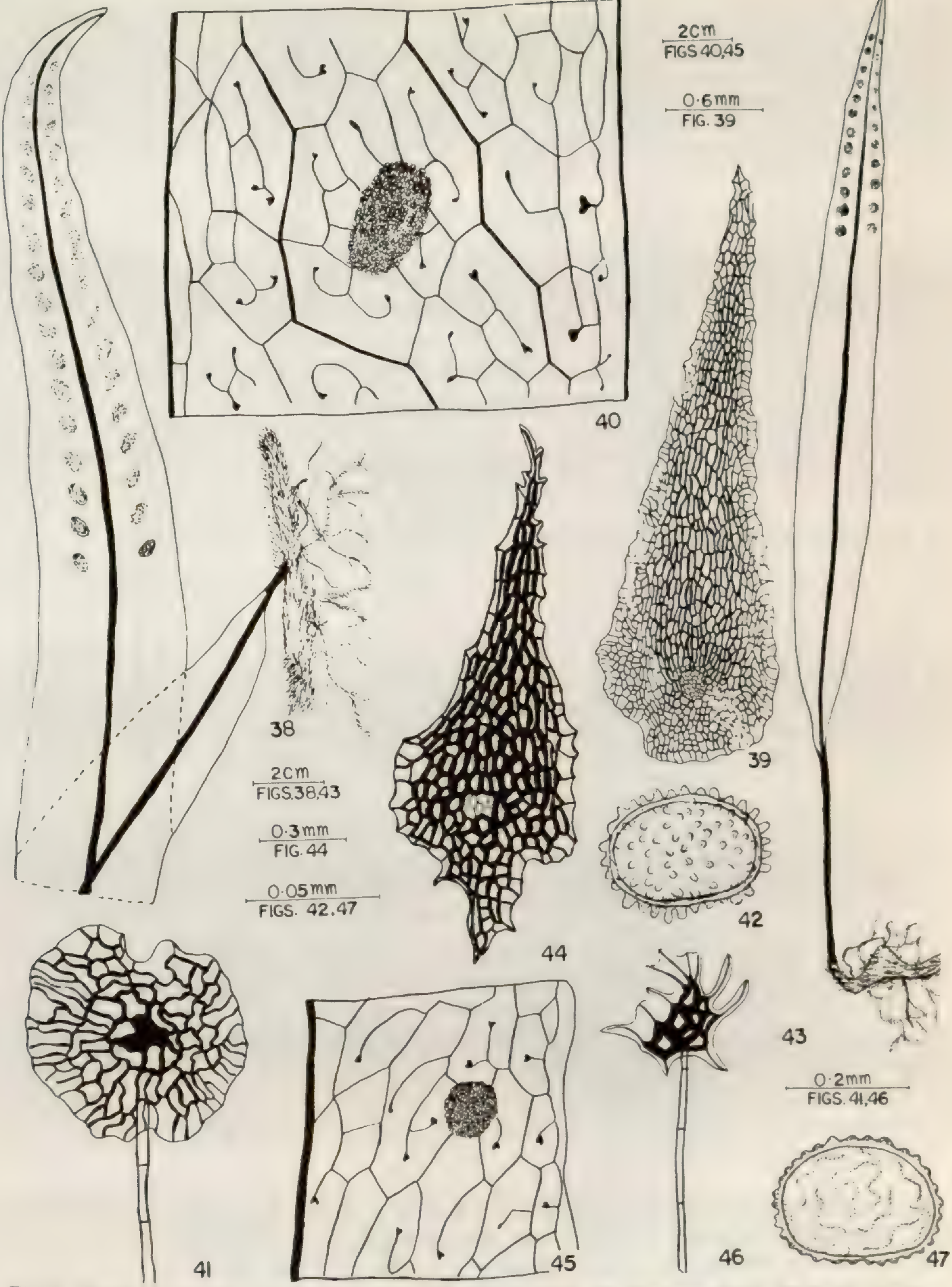
SPECIMEN EXAMINED:

THAILAND: Summit of Doi Chom Cheng, Doi Sootep mountains, 1500–1600 m, 1–6 Nov 1920, *Rock 1515* (US, a paratype of *P. oosphaerum* C. Chr.).

7. Lepisorus sordidus (C. Chr.) Ching, Bull. Fan Mem. Inst. Biol. 4: 78. 1933. Figs. 43–47.

Polypodium sordidum C. Chr. Contr. U. S. Nat. Herb. **26:** 320. 1931.
Pleopeltis sordida (C. Chr.) Panigrahi & Patnaik, Curr. Sci. **34:** 127. 1965.

Rhizome rather short-creeping, ca. 3 mm in diam., hypogeous, black, covered with a mass of fibrous roots, the young portions scaly, the scales 1–2 mm long, 0.5–0.8 mm wide, lanceolate with an acuminate apex, sparingly short-toothed, concolorous, blackish-brown to black, entirely opaque, rigid, the lumina of the cells small and narrow; fronds up to 0.25 cm distant, articulate to short pseudopodia; stipes 6.5–9 cm or more long, green-stramineous, sulcate above, glabrous; laminae 20–45 cm long, 2–3.5 cm wide below the middle, lanceolate, the



FIGS. 38–42. *Lepisorus oosphaerus*. FIG. 38. Frond. FIG. 39. Rhizome scale. FIG. 40. Lamina venation. FIG. 41. Sporangial paraphysis. FIG. 42. Spore. FIGS. 43–47. *L. sordidus*. FIG. 43. Frond. FIG. 44. Rhizome scale. FIG. 45. Lamina venation. FIG. 46. Sporangial paraphysis. FIG. 47. Spore.

apex acuminate, cuneate and short-decurrent at the base, grayish-green to yellow, often smoky, coriaceous, the venation hidden, glabrous except for a few, deciduous, black, ovate scales along the midrib; sori superficial, 3–4 mm in diam., globose, supramedial, uniseriate, usually confined to the upper half of the laminae; sporangial paraphyses black, clathrate, stellate, filiform; annulus 12–16-celled; spores hyaline to pale yellow, granulate, plano- or concavo-convex, globose to elliptic, 63–75 × 46–50 μm.

DISTRIBUTION: Eastern Himalayas, Burma, and Yunnan, China.

This large species is an epiphyte in the eastern Himalayas and has been collected from Laju, in the Tirap Frontier Division of the North Eastern Frontier Agency (NEFA), now Arunachal, at 1600 m altitude (Panigrahi & Patnaik, 1965). It greatly resembles both *L. sublinearis* and *Pleopeltis macrosphaera* var. *astrolepis* (Bir & Trikha, 1968a), but differs from both in its entirely black, opaque rhizome scales and in the smoky appearance of the fronds.

SPECIMEN EXAMINED:

CHINA: Yunnan: Between Tengueh and Lunging, Oct–Nov 1922, *Rock 7160* (US, holotype of *P. sordidum*).

8. Lepisorus subconfluens Ching, Bull. Fan Mem. Inst. Biol. 4: 83. 1933.

Figs. 48–52.

Polypodium neurodioides C. Chr. var. 4, Contr. U. S. Nat. Herb. **26:** 319. 1931, *nom. illeg.*
Pleopeltis subconfluens (Ching) Panigrahi & Patnaik, Curr. Sci. **34:** 127. 1965.

Rhizome creeping, ca. 2 mm in diam., densely scaly, the scales 2–3 mm long, 0.5–1 mm wide, linear-subulate with an ovate base, bicolorous, reddish-brown to blackish-brown, with thick-walled, dark colored cells in the center, the lumina narrow and elongate, the basal portion and margins hyaline, the margin dentate; fronds 2–4 mm distant; stipes 0.5–1 cm long, terete; laminae 10–20 cm long, 0.4–0.8 cm wide, linear-elongate, gradually acuminate at the apex, the margins rather narrowly revolute, greenish-brown, coriaceous, the venation obscure; sori submedial, elongate-oblong, approximate, more or less confluent near the lamina apex, mostly confined to the upper half of the laminae; sporangial paraphyses clathrate with an erose margin; annulus 13–15-celled; spores clear to pale yellow, reticulate-granulate, round to oval or elliptical, plano- or concavo-convex, 50–71 × 46–59 μm.

DISTRIBUTION: Eastern Himalayas, northern Thailand, and Yunnan, China.

This small, narrow-leaved species is found in the eastern Himalayas from the Kameng Frontier Division (NEFA) and from the Khasia Hills in Assam (Panigrahi & Patnaik, 1964).

SPECIMEN EXAMINED:

THAILAND: Summit of Doi Chom Cheng, Doi Sootep mountains, 1500–1650 m, 1–6 Nov 1920, *Rock 358* (US, det. K. Iwatsuki).

9a. Lepisorus amaurolepidus (Sledge) Bir & Trikha in Bir & Vasudeva, J. Bombay Nat. Hist. Soc. 68: 192. 1971, var. amaurolepidus.[4]

Pleopeltis amaurolepida Sledge, Bull. Brit. Mus. Nat. Hist. 2(5): 136. 1960.
Polypodium gladiatum Wall. Num. List. no. 279. 1828, *nom. nud., non P. gladiatum* Kunze, 1834.

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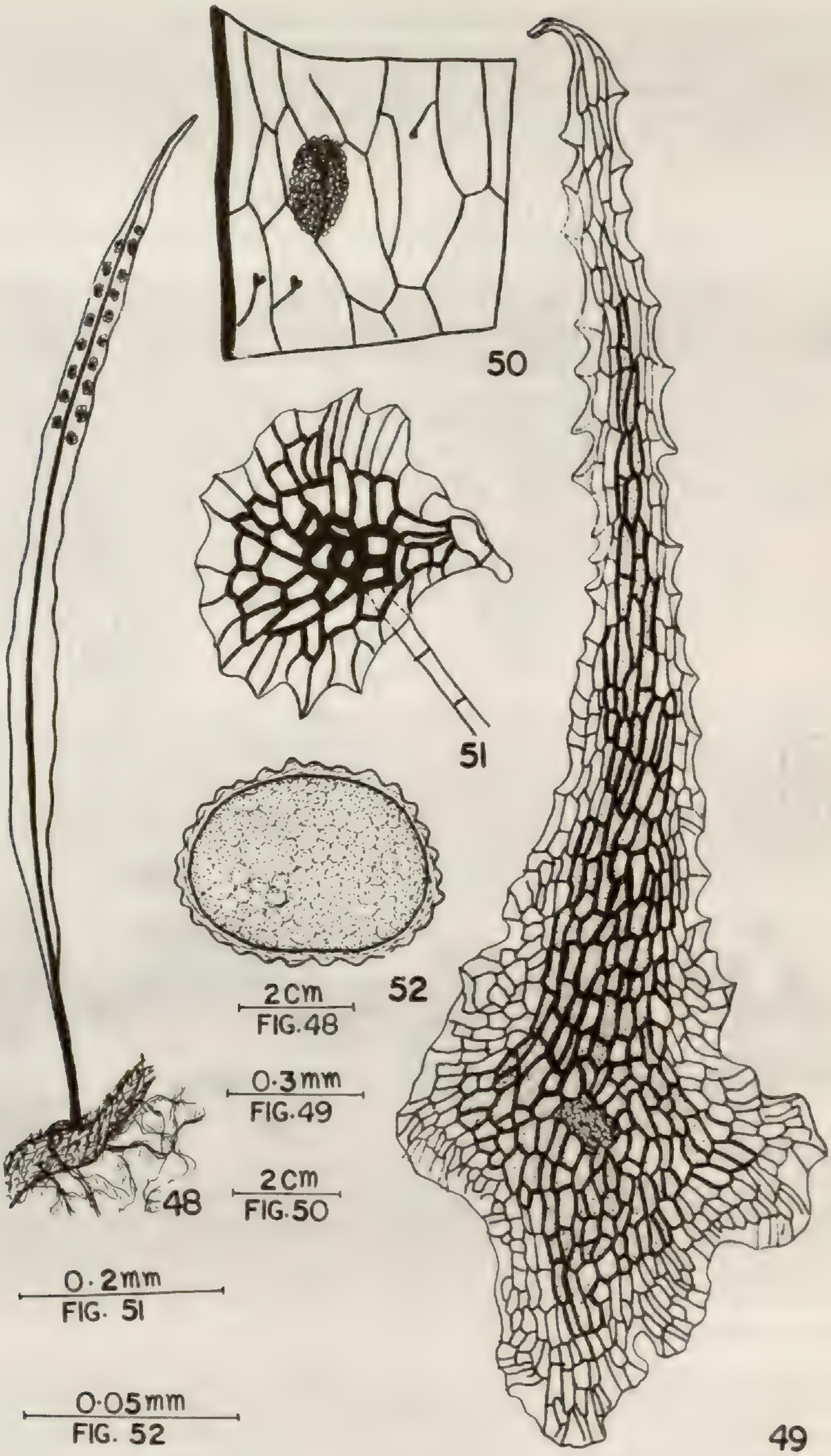
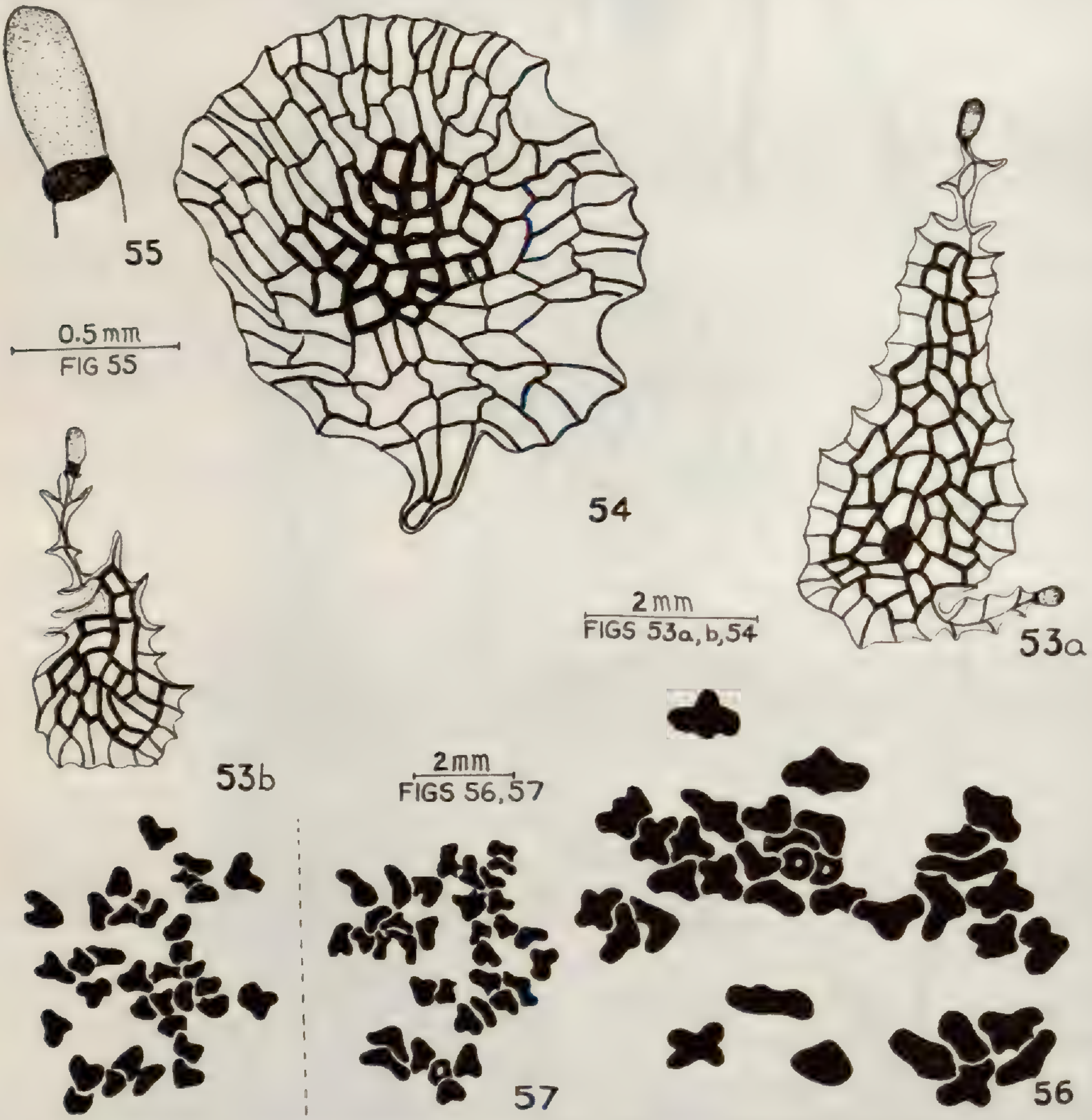
[4] For illustrations, see Bir & Trikha (1972, *f. 18–22*). Bir and Trikha (in Bir & Vasudeva, 1971) proposed the new combination incorrectly as *Lepisorus amaurolepida*.



FIGS. 48–52. *Lepisorus subconfluens*. FIG. 48. Frond. FIG. 49. Rhizome scale. FIG. 50. Lamina venation. FIG. 51. Sporangial paraphysis. FIG. 52. Spore.

Rhizome wide-creeping, 1.5–3 mm in diam., branched, densely scaly, the scales 2–3 mm long, 1–1.5 mm wide at the base, ovate-lanceolate, short-acuminate, firm, orbicular, peltate, bicolorous, dark brown, clathrate, the central cells highly thickened, blackish-brown, the cell cavities occluded, the margin dentate; stipes ca. 0.5–1 cm distant, 1–3 cm long, naked; laminae 6–25 cm long, 0.5–2 cm wide,



FIGS. 53–57. *Lepisorus amaurolepidus* var. *longifolius*. FIGS. 53a, b. Frond scales. FIG. 54. Sporangial paraphysis. FIG. 55. Hair-like sporangial paraphysis. FIG. 56. Spore mother cell at metaphase-I showing 35 bivalent chromosomes. FIG. 57. Spore mother cells at anaphase-I showing 35 chromosomes at each pole.

linear-lanceolate, gradually attenuate downward, the apex long-acuminate or rarely abruptly shortened and acute, light green or brown when dry, fleshy, the veins distinct, the areolae in 2 or 3 series between the midrib and the margin, both surfaces glabrous except for a few scales on the under surface along the midrib; sori 2–4 mm in diam., medial, golden brown; sporangial paraphyses with thickened and colored cell walls, without glandular cells when young; spores yellow, plano- or concavo-convex, sometimes reniform, the exine thick, 48–58 × 29–42 μm.

DISTRIBUTION: Himalayas, Central India, South India, and Ceylon.

This is the commonest species of *Lepisorus* in South India in the Palni and Nilgiri Hills at 1500–2000 m altitude. It is also known from Mahableshwar, Coorg, Coimbatore, and Kerala State, and is occasionally found in the central Indian mountains at Pachmarhi (Madhyra Pradesh) and in the Himalayas. For details of specimens examined, see Bir & Trikha (1972).

9b. Lepisorus amaurolepidus var. longifolius Bir & Trikha, var. nov.

Figs. 53–57.

Frondae eis var. *amaurolepidi* longiores, 26–35 cm longae, 1–1.5 cm latae; laminae subtus paleaceae, paleis deciduis, clathratis, rufo-brunneis, margine dentatis, dentibus prominentibus, cellula apicali juventute glandulari; paraphyses dimorphae, nonnullae circulares, peltatae, margine fere integro, alterae piliformes, 2-cellulares; sporae laeves vel rugoso-verrucosae, 41–61 × 35–48 μm; $n = 35$.

TYPE: Nainital–Ranikhet bridle path, western Himalayas, abundant on rocks, 900–1200 m altitude, July 1971, *Trikha 1911* (PUN 1130; isotypes PUN 1131, 1132).

This variety differs from var. *amaurolepidus* in its larger fronds, in the presence of 2-celled, hair-like sporangial paraphyses, and in the scales on the under surface of the laminae.

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SHORTER NOTE

THE CORRECT NAME OF A LYCOPODIUM NEW TO PANAMA.—A species of the *Lycopodium cernuum* group new to Panama was found on August 25, 1972 at the summit of Cerro Jefe, about 15 km northeast of Panama City in the Province of Panama at an elevation of 900 m (*M. D. Correa et al. 1796,* MO fragm US). This specimen is conspecific with others from Venezuela, Columbia, Ecuador, Peru, and Bolivia. It is more compact and robust than most specimens of *L. cernuum,* and unlike *L. cernuum* it has pubescent stems and sometimes a few cilia on the leaf margins. The species resembles the Brazilian *L. eichleri* Glaziou ex Fée, which also has pubescent stems. But *L. eichleri* is more erect, has narrower dichotomies, is less robust, and has non-ciliate leaves with white, translucent, thin, greatly prolonged apices. In Peru and Bolivia some specimens agreeing in pubescence and leaf morphology with the Panama specimen have the weeping branchlet habit of *L. pendulinum* Hooker. The latter, however, does not have pubescent stems. The taxonomic status of these specimens is an open question.

This Andean–Panamanian species was originally known as *Lycopodium capillaceum* Willd. *in herb.*, based on *Humboldt 473* from Guanaguana, Edo. Monagas, Venezuela (B-Hb. Willd. 19429). A microfiche in the Smithsonian Institution Library shows a brief description attached to the sheet, but this was not published by Willdenow. Spring (Flora **21:** 165. 1838) published the name in synonymy—and therefore invalidly–as *L. capillaceum* Willd. ex Spring. Shortly thereafter, Spring (Monogr. Lycopod. **1**: 80. 1842) validly published the name *L. cernuum* var. *capillaceum,* again based on the Humboldt specimen. Hieronymus (Bot. Jahrb. Engler **34**: 573. 1905) attributed the specific combination erroneously to "Willd. [in] Spring in Flora XXI," overlooking the fact that the name was published there in synonymy. Since he also cited Spring's validly published variety, Hieronymus actually made the correct, if inadvertent, new combination at the species level, which should be cited as: *L. capillaceum* (Spring) Hieron.—*David B. Lellinger, U. S. National Herbarium, Smithsonian Institution, Washington, D. C. 20560.*

REVIEW

"IDENTIFICATION OF THE 'AIR FERN' SOLD IN THE UNITED STATES," by A. O. and Sharon S. Tucker, Baileya **19**: 114–115. 1974.—Perhaps the most novel "plant" sold on a large scale in the United States is the "Air Fern," which has bright green, bluish green, or magenta, plumose "fronds" with highly divided, almost dichotomously branched "pinnae." Among the claims made for this novelty is that it grows on air and needs no soil or water. The authors identify the "Air Fern" as the dyed remains of the marine animal *Sertularia argentea* L., a colonial hydroid of the phylum Coelenterata. It is dredged from the estuary of the River Thames at the English Channel, dried, and dyed for sale. Because it is non-living, it makes an attractive decoration for dark places where living ferns will not grow.—*D.B.L.*

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Some Aspects of the Ecology of Ophioglossum engelmannii in the Cedar Glades of Kentucky and Tennessee

JERRY M. BASKIN and CAROL C. BASKIN*

Ophioglossum engelmannii Prantl (Ophioglossaceae) is a North American fern whose reported geographical range extends from Florida to Arizona and south-central Mexico north to northwestern Virginia, southern Ohio, southern Indiana, Missouri, Kansas, and Oklahoma. Plants of this species have been found growing in prairies, in open, grassy woodlands, on bluffs, in clay barrens, and in cedar (limestone) barrens and glades (Clausen, 1938; Fernald, 1950). Throughout its range, *O. engelmannii* is restricted to limestone soils, and thus Palmer (1932) considered it a strict calciphile. In a study of its soil reaction preferences, Wherry (1926) found that *O. engelmannii* is restricted to soils with a neutral to slightly alkaline pH. Information on macro-geographical distribution and general habitats of the species, as well as taxonomic data, can be found in several taxonomic works (Clausen, 1938; Fernald, 1950; Shaver, 1954; Gleason, 1952). The anatomy of the vegetative organs, as well as some aspects of sexual reproduction, also have been studied (Bold, 1967). Although this unusual fern is of much interest to botanists, little information is available on its autecology. Thus, the purpose of this paper is to report (1) observations made on the ecology of *O. engelmannii* in cedar glades of Kentucky and Tennessee, with special reference to its vegetative life cycle and (2) results of laboratory studies on the temperature relations of bud growth and dormancy.

DISTRIBUTION, HABITAT, AND PLANT ASSOCIATES

In Kentucky *O. engelmannii* has been reported from Barren, Boone, Calloway, Clark, Edmonson, Logan, Marshall, Rockcastle, Simpson, Warren, and Wayne Counties (Braun, 1936; Reed, 1958; McCoy, 1938; McCoy & Hunter, 1968), and we have found it in Bullitt County, making a total of 12 counties in which the species is known to occur. Shaver's (1954) map of its distribution in Tennessee shows that the species occurs in Bedford, Davidson, Decatur, Franklin, Knox, Marion, Marshall, Maury, Montgomery, Rutherford, Smith, Williamson, and Wilson Counties. Specimens from Hamilton and Meigs Counties are in the University of Tennessee herbarium (A. M. Evans, pers. comm.). In addition, we have found it growing in Sumner and Giles Counties, making a total of 17 counties in Tennessee (*Fig. 1*).

In both states the populations of *O. engelmannii* are restricted to areas with shallow, limestone soils (cedar glades or cedar barrens). Some populations occur on relatively large, well-developed cedar glades (e.g., those in Bullitt and Simpson Counties, Kentucky and Marshall, Rutherford, and Wilson Counties, Tennessee), where *O. engelmannii* grows in association with a number of characteristic herbaceous cedar glade species. However, other populations occur on small rock

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outcrops, where *O. engelmannii* may be associated with only one or two characteristic cedar glade species.

Within the cedar glades, plants of *O. engelmannii* usually are found growing on the open glades (i.e., areas where the soil is too shallow to support shrubs or trees), although occasionally they grow at the edges near deciduous shrubs. Soil depths in open glades range from 0 to 25 cm and occasionally up to 50 cm in deep, soil-filled cracks. Plants of *O. engelmannii* generally are restricted to soil that is 5–15 cm deep, but they are most abundant in soil that is 10–15 cm deep. In glades developed on thin-bedded limestone, soil has accumulated among rock fragments and in crevices; in glades developed on thick-bedded limestone, a layer of soil has formed over a massive bed of limestone. In both types of glades the soil is saturated with water during late autumn, winter, and early spring, but during late spring, summer, and early autumn it is subject to long periods of drought.

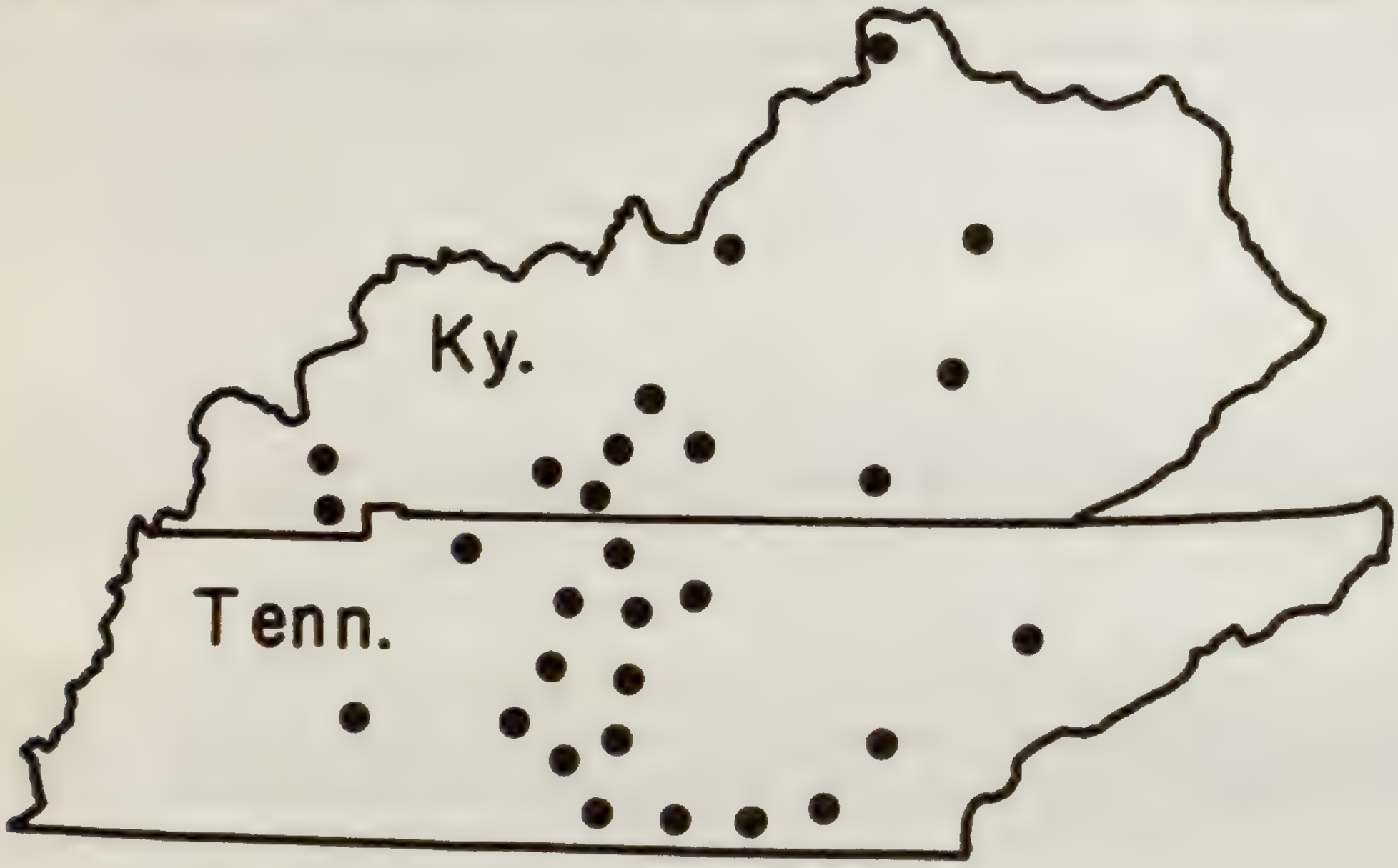

FIG. 1. Geographical distribution of *O. engelmannii* in Kentucky and Tennessee.

The most common and abundant associate of *O. engelmannii* in the cedar glades of Kentucky and Tennessee is the summer annual, xerophytic grass *Sporobolus vaginiflorus*. This grass is the dominant species in much of the open glade community (Baskin & Baskin, 1973). Other common associates in the cedar glades include *Ruellia humilis, Scutellaria parvula, Nothoscordum bivalve, Heliotropium tenellum, Agave virginica, Petalostemon gattingeri* (in central Tennessee), and *Diodia teres* (in Bullitt County, Kentucky).

In the Ozark Region of Arkansas and Missouri *O. engelmannii* grows on limestone ledges or glades in shallow soil that is saturated with water in spring but which later becomes quite dry. The species also occurs on clay and gravel banks, but always in calcareous soil (Palmer, 1932). In a shallow-soil habitat on Mississippian limestone in Missouri, Palmer (1914) lists the following species as associates of *O. englemannii: Bouteloua curtipendula, Allionia albida, Tragia ramosa, Malvastrum angustum, Sedum pulchellum,* and *Opuntia* sp. Elsewhere,

O. engelmannii has been found growing in prairie-like situations and in association with prairie species. Braun (1927) described this kind of habitat in Ohio and listed the following associates: *Andropogon scoparius, Bouteloua curtipendula, Agave virginica, Lithospermum canescens, Senecio balsamitae* and *Blephilia ciliata*.

PHENOLOGY

Phenological observations were made on *O. engelmannii* in the middle Tennessee cedar glades from April 1969 to September 1973 and in the Kentucky glades from March 1972 to September 1973. Some observations were made on populations in four counties in Kentucky and eight in Tennessee, but the most detailed observations were made on populations growing in Bullitt and Simpson Counties, Kentucky and in Rutherford and Wilson Counties, Tennessee. Most of the observations on bud growth were made in a glade in Bullitt County, Kentucky that had been surveyed for development and was later destroyed.

Plants of *O. engelmannii* have a short, vertical rhizome about 0.5 cm long, the top of which is 1–2 cm below the soil surface. This rhizome is attached to the upper side of a large, straight, horizontal root that often extends 5 to 10 cm on both sides of the rhizome. According to Bold (1967) and Shaver (1954), this basal root produces adventitious buds which develop into new plants, resulting in the production of large colonies of asexually produced plants. We have observed this many times in the field. From the sides of the erect rhizome arise 5–15 unbranched roots that, for the most part, grow horizontally. Leaf buds are produced at the rhizome apex. A complete leaf consists of a sterile leaflet (blade) and a stalked, spike-like fertile leaflet (fertile spike). A single plant can produce one or two leaves at a time, and the leaf (or leaves) may or may not be fertile. The leaves turn green long before they reach the soil surface, indicating that light is not required to produce chlorophyll.

To determine the number of plants that produce (1) one leaf, (2) one leaf and one fertile spike, (3) two leaves, and (4) two leaves and two fertile spikes, a total of eleven 1-meter square quadrats were established in four cedar glades in Tennessee and Kentucky, and all the plants in each of them were examined for number of leaves and fertile spikes (*Table 1*). A total of 2,869 plants were present in the 11 quadrats, and of these 2,367 (82.5%) had one leaf and 502 (17.5%) had two leaves. The smallest number of plants per quadrat with two leaves was 19 (7.5%) and the largest was 101 (44.7%). Only 292 (10.2%) of the 2,869 plants had fertile spikes and only 43 (1.5%) of the plants had two fertile spikes. No plants with one fertile and one sterile leaf on the same rhizome were present in the quadrats. However, in May 1974 we saw a few plants with one fertile and one sterile leaf in Simpson County, Kentucky and in Rutherford County, Tennessee.

Leaves begin to emerge from the soil in mid March, and by mid April they are fully expanded. In plants that produced a fertile spike, it is inside the rolled blade as it emerges from the soil. The spike does not elongate as fast as the leaf, and thus does not reach its full length until late April. Sporangia begin releasing spores during the first week of May, and by the first week in June all of them have been released. During drier years or in drier microhabitats all of the spores may be

released within two weeks. The leaves begin to turn yellow in mid-May, and by late May and early June, depending on habitat moisture, the plants are dormant.

All plants in a population produce leaves in the spring, but in late summer and autumn only a few leaves emerge, and only a few of these are fertile. The number of leaves that emerges appears to be related to soil moisture. In years with wetter summers and autumns or in wetter habitats in the same year, more leaves emerge than in drier years or in drier habitats. The leaves that emerge during summer and autumn are killed before winter, and the plants are dormant during the winter. Leaves that emerge during wet periods in August may be killed during late summer or early autumn by drought; or if soil moisture permits, they may remain green until killed by low temperatures in late autumn. Those that emerge in early autumn generally are killed by low temperatures in late autumn, rather than by drought.

TABLE 1. NUMBER OF LEAVES AND FERTILE SPIKES ON PLANTS OF *O. ENGELMANNII*.

Location & date	*Quad. No.*	*Total No. Pls.*	*1 leaf & no spike*		*1 leaf & 1 spike*		*2 leaves & no spike*		*2 leaves & 2 spikes*	
			No.	*%*	*No.*	*%*	*No.*	*%*	*No.*	*%*
Bullitt County, Ky.	1	236	158	66.9	22	9.3	51	21.6	5	2.1
6 May 1973	2	436	379	86.9	22	5.0	35	8.0	0	0.0
	3	444	387	87.2	16	3.6	37	8.3	4	0.9
	4	127	84	66.1	3	2.4	39	30.7	1	0.7
	5	235	189	80.4	5	2.1	41	17.4	0	0.0
Simpson County, Ky.	1	253	204	80.6	30	11.9	19	7.5	0	0.0
15 May 1973	2	383	276	72.1	71	18.5	31	8.1	5	1.3
Rutherford County,	1	146	71	48.6	25	17.1	46	31.5	4	2.7
Tenn. 15 May 1973	2	291	237	81.4	21	7.2	30	10.3	3	1.0
Wilson County, Tenn.	1	92	55	59.8	7	7.6	29	31.5	1	1.0
16 May 1973	2	226	78	34.5	27	11.9	101	44.7	20	8.8
Totals	11	2,869	2,118	73.8	249	8.7	459	16.0	43	1.5

Autumn emergence of leaves and fertile spikes of *O. engelmannii* has been reported in the Ozark Region of Missouri and Arkansas (Palmer, 1932), near Norman, Oklahoma (Couch, 1937), and in eastern Kansas (Magrath & Weedon, 1972). Palmer (1932) and Couch (1937) indicated that autumn growth was associated with periods of high soil moisture, just as it is in the cedar glades of Kentucky and Tennessee.

By the time a leaf is fully expanded, in either spring or autumn, a new leaf bud is present on the rhizome at the base of the petiole of the expanded leaf. To follow the growth of shoot buds produced in spring, 80 plants were removed from the Bullitt County population at irregular intervals from June 1972 until February 1973. The length of each bud was measured to the nearest millimeter; lengths of buds collected on various dates are given in *Table 2*. The buds that were measured in November, January, and February are buds that were initiated the previous spring. Because the autumn of 1972 was dry, very few plants in the population had leaves to emerge; therefore, new buds were not produced. Although bud

growth was slow, some did occur during summer, autumn, and winter; there was no period of rapid extension. The tips of buds collected on 25 February 1973 had almost reached the soil surface. By 19 March the leaves had emerged and were 2–4 cm above the soil surface.

TEMPERATURE RELATIONS OF BUD DORMANCY AND GROWTH

Phenological events in the vegetative life cycle of *O. engelmannii* are related directly to bud growth and dormancy. In order to understand the vegetative life cycle of this species, external and internal factors controlling bud growth and dormancy should be identified.

In the cedar glade habitat, soil moisture is not a limiting factor in the growth of *O. engelmannii* from mid-autumn to mid-spring; it may or may not act as a limiting factor from mid-spring to mid-autumn. Obviously, if the habitat is very dry, soil moisture will limit growth, even if buds are physiologically non-dormant and other external factors are optimum for growth.

TABLE 2. GROWTH OF BUDS OF *O. ENGELMANNII* IN CEDAR GLADES.

Collection date	*Mean length* ± SE (mm)
5 June 1972	3.3 ± 0.2
3 July 1972	3.5 ± 0.3
7 Aug. 1972	5.2 ± 0.3
24 Nov. 1972	8.9 ± 0.3
21 Jan. 1973	10.3 ± 0.4
25 Feb. 1973	11.1 ± 0.4

Under non-limiting soil moisture conditions, temperature and light are the two most important external factors controlling vegetative growth of plants in their natural habitats. Since the buds of *O. engelmannii* are below ground and are physiologically non-dormant when they emerge above ground, light can be ruled out as a factor that breaks dormancy or initiates growth in this species. Thus, it would appear that temperature controls bud dormancy and growth and the seasonal vegetative life cycle of this species.

This study was restricted to temperature relations of bud dormancy and growth of buds formed in spring. All plants used in the experiments were collected from the cedar glade in Bullitt County, Kentucky that since has been destroyed. As mentioned above, it was very dry in this glade during autumn of 1972. As a result, very few of the plants produced summer buds; almost all of the buds in the population were spring-formed.

The purpose of the first experiment was to determine if buds are innately dormant when the spring-formed leaves die in late spring or if they remain quiescent due to temperatures and/or soil moisture conditions that are unfavorable for leaf emergence. On 5 June 1972, 160 plants were collected from the glade and each plant was placed on a 5 cm layer of moist sand in a styrofoam cup with drainage holes in the bottom. The plants were only partially covered with sand so that the buds could be examined and measured to the nearest millimeter without disturbing the plants. Twenty plants were placed in each of eight enamel trays, and then the trays were wrapped with aluminum foil to provide darkness. A tray containing

20 plants was placed at each of four constant temperatures (10, 15, 20, and 25° C) and four alternating temperatures (15/6, 20/10, 30/15, and 35/20° C) in temperature-controlled incubators. The alternating temperature regimes (12/12 hr thermoperiods) were selected to represent the mean daily maximum and minimum monthly temperatures that might occur in the *O. engelmannii* habitat during the growing season. The temperatures used and the month(s) to which these correspond are: March 15/6° C, April 20/10° C, May 30/15° C, June 30/15° C, July 35/20° C, August 35/20° C, September 30/15° C, October 20/10° C, and November 15/6° C. These temperatures closely approximate soil temperatures 2.5 cm below bare ground on a flat surface in Lexington, Kentucky for the respective months given (Jerry Hill, pers. comm.). Bud length on each plant was measured to the nearest millimeter at 5-day intervals in a darkened room with the aid of a green safe light, and the sand was watered, if needed, while the plants were exposed to the green light.

TABLE 3. GROWTH OF NEWLY INITIATED BUDS OF *O. ENGELMANNII* AT CONSTANT AND ALTERNATING TEMPERATURES IN THE LABORATORY.

Temp. (°C)	*Mean length* ± SE *initial*	*Mean length* ± SE *after 30 days*	*Difference*
10	3.7 ± 0.5 mm	3.9 ± 0.6 mm	0.2 mm
15	2.8 ± 0.3	3.3 ± 0.2	0.5
20	2.8 ± 0.3	3.1 ± 0.2	0.3
25	3.6 ± 0.5	4.1 ± 0.5	0.5
15/6	2.7 ± 0.3	2.7 ± 0.3	0.0
20/10	3.1 ± 0.2	3.8 ± 0.5	0.7
30/15	3.9 ± 0.6	5.0 ± 0.8	1.1
35/20	3.2 ± 0.4	3.8 ± 0.4	0.6

In late spring and early summer, buds of *O. engelmannii* are innately dormant (*Table 3*). That is, the lack of leaf emergence is due to some physiological factor(s) within the bud and not to environmental conditions. Although some growth (1.1 mm or less) occurred at all temperatures tested except 15/6° C, it was not nearly enough to bring the leaf above the soil surface. A bud would have to grow 1–2 cm before the tip of the leaf would be above the soil surface.

To study the influence of temperature on shoot emergence in freshly dormant plants, 20 plants collected on 5 June 1972 were placed at each of the four constant and four alternating temperatures. Each plant was planted in greenhouse potting soil in a styrofoam cup, and the top of the rhizome was 2 cm below the soil surface. The soil in each cup was kept moist, and the cups were checked for emergent leaves at 10-day intervals from 5 June until 12 November 1972. A leaf was considered to have emerged when its tip was 0.5 cm above the soil surface.

Leaves of some of the plants at 35/20, 30/15, 20/10, and 25° C emerged (*Fig. 2*). Leaf emergence was greatest at 35/20 and 30/15° C, where 18 and 16 leaves, respectively, came above the soil. For the most part emergence began in late July and continued into early October. On 12 November, ten of the plants at 10, 15, 15/6, and 20/10° C that had not produced an emergent leaf were placed at 30/15° C for 30 days. About half of the plants at 30/15° C produced leaves (3,4,6, and 6 of the plants removed from 10, 15, 15/6, and 20/10° C, respectively); whereas, only three of those left at the original temperatures produced leaves (2 at 10° C and 1 at

15° C). Thus, it appears that although high temperatures are not absolutely necessary to overcome dormancy, buds lose their dormancy much faster at high than at low temperatures. Also, high temperatures are required for growth after the buds are no longer dormant.

To obtain information on the influence of winter field conditions on rate of shoot emergence and the temperatures required for shoot emergence, 80 plants were collected in the field on 21 January and 25 February 1973, and 20 plants were placed at each of the four alternating temperature regimes. Plants were potted in soil with the buds covered to a depth of 2 cm. The soil was kept moist throughout the experiment. The cups were checked for emergent leaves at 5-day intervals for about 2 months.

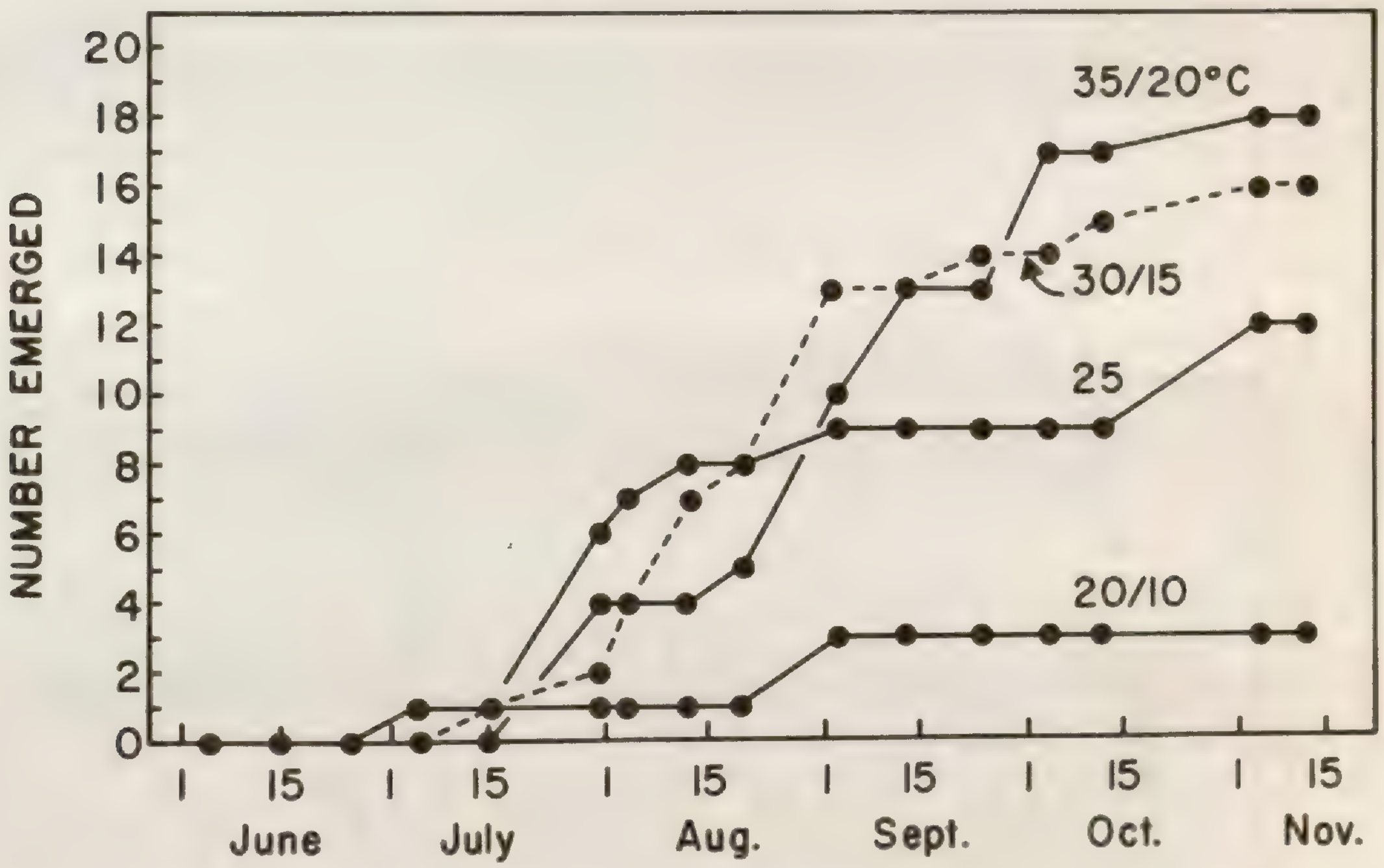

FIG. 2. Effect of temperature on leaf emergence of *O. engelmannii*. Freshly-dormant plants were planted in soil on 5 June 1972. There was no emergence at 10, 15, 20, and 15/6°C.

At 30/15 and 35/20° C essentially all of the leaves of plants from both collection dates emerged after 15 days (*Fig. 3*). Emergence at 20/10 and 15/6° C, however, was much slower, and, except for plants collected in January and placed at 20/10° C, the number of leaves that came up was reduced by 50% or more. At 20/10° C, 17 of the January-collected plants produced leaves; whereas, only 10 of the February-collected plants did so. At 15/6° C there was a marked increase in rate as well as number of leaves that emerged in the February-collected plants as compared to the January-collected plants. Thus, it appears that although rate of leaf emergence is slow, leaves will grow at low temperatures (15/6° C) after they have overwintered in the field.

DISCUSSION

Freshly dormant buds of *O. engelmannii* are innately dormant, as indicated by their small amount of growth over a wide range of constant and alternating temperatures (*Table 3*). However, after a short period of dormancy in the field, buds gain the ability to grow slowly at high temperatures (*Table 2*), and if soil moisture conditions permit, some of the plants produce emergent leaves in late summer and early autumn. Thus, soil moisture in the habitat during this period appears to be a major factor determining shoot emergence. On the other hand, leaf emergence is prevented in late autumn when the soil is moist because temperatures are below those required for growth. Apparently, during the low temperature winter period changes occur in the physiological state of the plants that render them capable of growing at lower temperatures than non cold-treated plants. Whereas plants collected from the field in late November and placed at 20/10 and 15/6° C (the simulated October and November temperatures) did not have emergent leaves after two months (Baskin & Baskin, unpub.), plants collected in late February and placed at 20/10 and 15/6° C had emergent leaves after 9 and 33 days, respectively (*Fig. 3*).

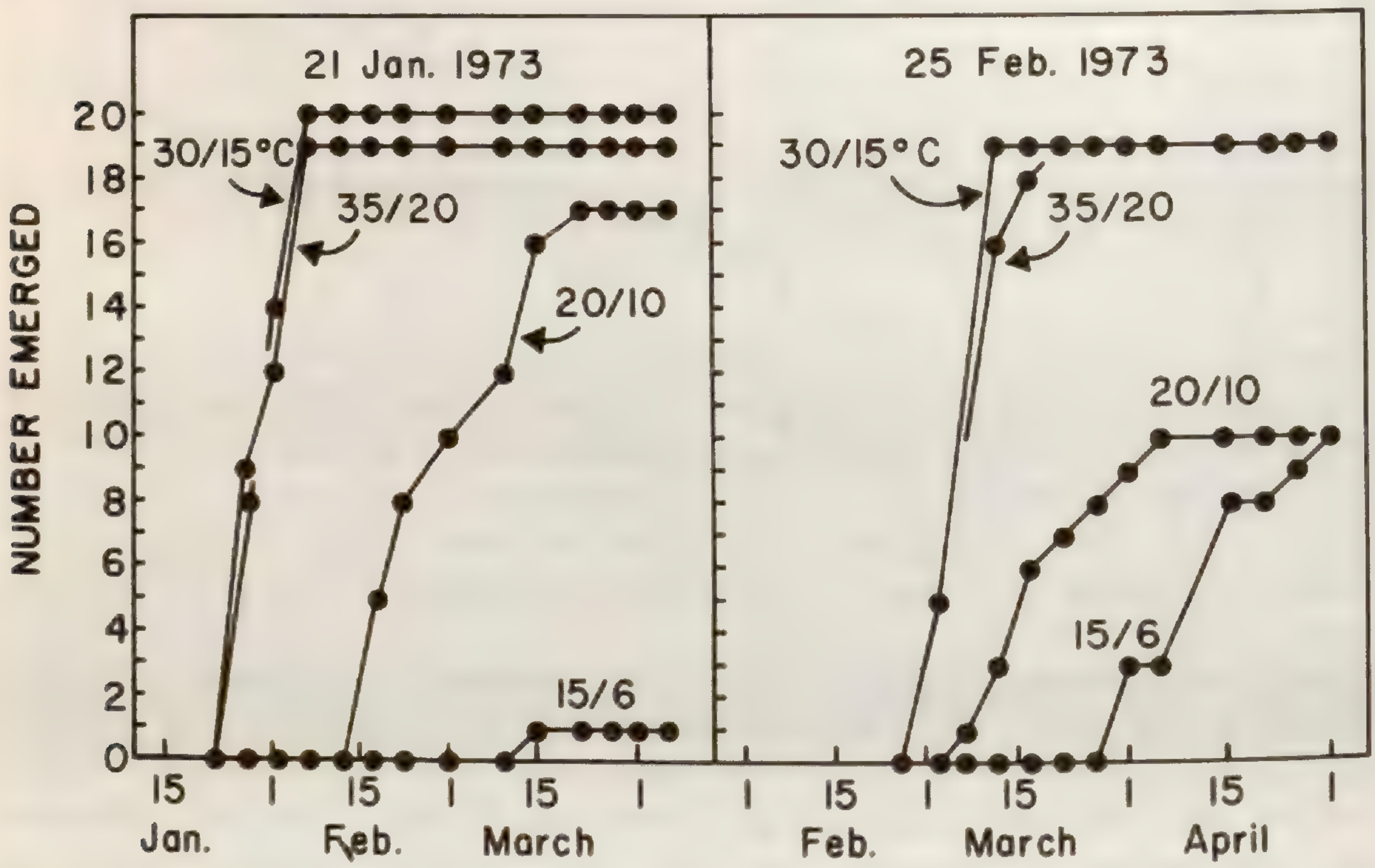

FIG. 3. Leaf emergence of *O. engelmannii* plants at four alternating temperatures. Plants were collected in the field on 21 January and 25 February 1973.

Following the models proposed by Vegis (1963, 1964) for breaking of dormancy in seeds and buds of plants, the emergence of *O. engelmannii* buds from dormancy can be summarized as follows. Newly formed buds are innately dormant when leaves that emerged in spring die in late spring and early summer. From this state of innate dormancy, the buds pass into a state of conditional dormancy when

they will emerge only at high temperatures and at a relatively slow rate. Finally, after a winter period of low temperatures, the buds become completely non-dormant and thus are capable of growing and emerging at a fast rate over a wide range of temperatures.

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A Newly Recognized Gleichenia Hybrid from Cuba

J. J. DUEK*

While preparing a revision of the *Gleichenia* family for the Cuban fern flora, I found a species that I think is a hybrid, for all specimens of it that I have examined appear to be sterile, with few sporangia and abortive spores. This species was first described by Maxon as *Dicranopteris leonis*. In the arrangement of the Gleicheniaceae made by Holttum (1957), it belongs in *Gleichenia* subg. *Mertensia* (Willd.) Holttum (see also Holttum, 1973). I postulate that the parents of this hybrid are *Gleichenia bifida* and *G. palmata*. The nomenclature and distribution of these species are as follows:

Gleichenia bifida (Willd.) Spreng. Syst. Veg. ed. 16, 4: 27. 1827.

Mertensia bifida Willd. Kongl. Vetensk. Acad. Nya Handl. 11(25): 168, *t. 5, f. B.* 1804. TYPE: Caracas, Venezuela, *Bredemeyer* (B!).

DISTRIBUTION: Cuba, Jamaica, Hispaniola, Puerto Rico, St. Kitts, Montserrat, Guadeloupe, Trinidad, Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Colombia, Venezuela, Brazil, and Bolivia.

SELECTED SPECIMENS CITED:

CUBA: Oriente: Prope villam Monte Verde dictam, *Wright 921, p. p.* (B, BM, P, US); Pinar de Mícara, in pineland thickets, ca. 750 m, *Ekman 15895* (B, BM); La Prenda, ca. 800 m, *Eggers 5210* (B, P, US); Loma del Gato, *Clemente 654* (P); Sierra Maestra, Pico Suecia, ca. 1700 m, *Samek & Duek 1517* (IBH[1]). **Las Villas:** Buenos Aires, ca. 750–840 m, *Jack 6512* (IBS[1]); Trinidad Mountains, Santa Clara, Aguacate, ca. 750–850 m, *Britton & Wilson 5405* (US). **Pinar del Rio:** Environs of Sumidero, *Shafer & León* 13622 (P); Sierra de los Organos, San Diego de Tapias, in a small savanna, *Ekman 10645* (US).

Gleichenia × leonis (Maxon) C. Chr. Ind. Fil. Suppl. 3: 106. 1934, pro. sp.

Figs. 1, 2.

Dicranopteris leonis Maxon, J. Washington Acad. Sci. **12**: 439. 1922. TYPE: Pico Turquino region, Sierra Maestra, Pcia. Oriente, Cuba, *León 11092* (US!)

DISTRIBUTION: Provincia de Oriente, Cuba.

SPECIMENS CITED:

CUBA: Oriente: Sierra Maestra, on the divide between Punta de Palma Mocha and the pass between the Río Yara and the Río La Plata, ca. 1200 m, *Ekman 5585* (B, S, US); In the Maestrica, near the Batey "Alto de la Valenzuela," ca. 1300 m, *López Figueiras 2025* (UO[1]); 16° W from Pico Turquino, ca. 1920 m, basalt-like soil, *Samek & Duek 933* (IBH); Behind Pico Cuba, ca. 1840 m, *Samek & Duek 794* (IBH); 25° E from Pico Turquino, ca. 1970 m, *Samek & Duek 1186* (IBH); At the summit of Pico Cuba, ca. 1994 m, in dark brown, basaltic soil, *Samek & Duek 1292* (IBH); 20° SW from Pico Cuba, ca. 1820–1870 m, *Samek & Duek 962* (IBH).

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[1]The herbarium IBH was created in 1965 at the Institute of Biology, Dept. of Forest Ecology, Academy of Sciences of Cuba, La Habana, by Dr. V. Samek of the Academy of Sciences of Czechoslovakia, when I collaborated with him in 1964–1967. The following acronyms also are not in the fifth edition of "Index Herbariorum:" IBS Botanical Garden at Soledad, Cienfuegos, administered by the Institute of Botany, Academy of Sciences of Cuba (formerly Atkins Institution of the Arnold Arboretum); and UO Herbarium of the University of Oriente, Santiago de Cuba (now in HAJB). See Duek (1971).

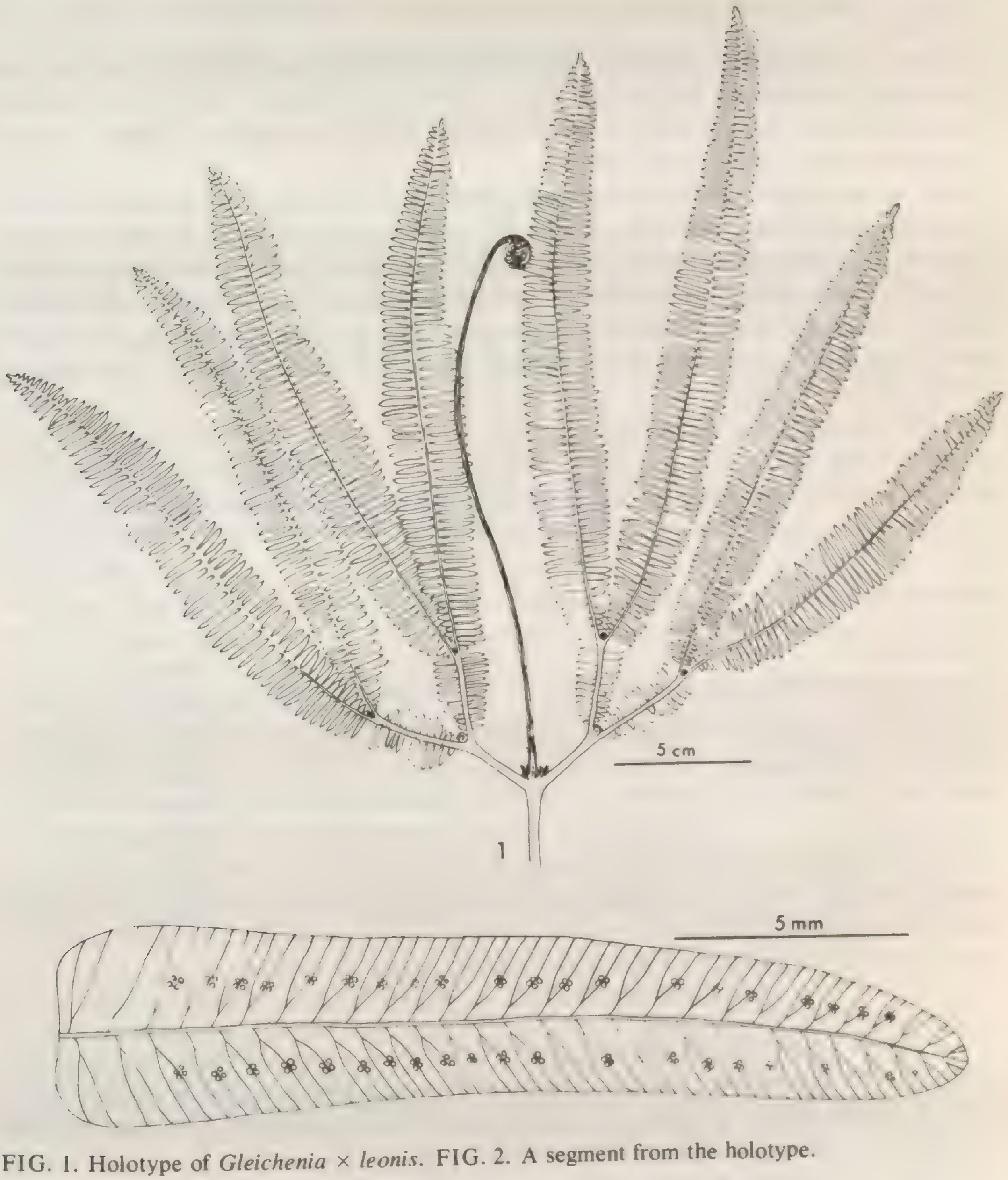

FIG. 1. Holotype of *Gleichenia* × *leonis*. FIG. 2. A segment from the holotype.

Gleichenia palmata (Underw.) C. Chr. Ind. Fil. Suppl. 1: 113. 1913.

Mertensia palmata Schaffn. ex Fée, Mém. Foug. **9**: 32. 1857, *nom. nud.*

Gleichenia palmata Moore, Ind. Fil. 380. 1862, *nom. nud.*

Dicranopteris palmata Underw. Bull. Torrey Bot. Club **34**: 259. 1907. TYPE: Orizaba, Edo. Veracruz, Mexico, *Pringle 6129* (US!)

Sticherus palmata (Underw.) Copel. Gen. Fil. 28. 1947.

DISTRIBUTION: Cuba, Jamaica, Mexico, and Guatemala.

SELECTED SPECIMENS CITED:

CUBA: Oriente: Gran Piedra, ca. 1500 m, *Shafer 9054* (P, S); Loma del Gato, ca. 1100 m, in

"fangales," *Ekman 6988* (S, US); Upper slopes and summit of Gran Piedra, ca. 900–1200 m, *Maxon 4036* (US).

That *Gleichenia* × *leonis* is intermediate in frond morphology from the two presumed parents can be seen in *Figs. 1* and *2*. In addition, *Table 1* lists characters of the three species; these show that the hybrid resembles *G. bifida* in some respects and *G. palmata* in others.

Although *G.* × *leonis* is known only from Cuba, it is to be expected in Jamaica, Mexico, and Guatemala. Judging by the specimens in the U. S. National Herbarium, however, the parents grow in close proximity more commonly in Pcia. Oriente, Cuba, than elsewhere. But both were collected near the Finca Sepacuite, Depto. Alta Verapaz, Guatemala, and near Betaza, Depto. Oaxaca, Mexico. In the latter locality, *G. bifida* was found at 4750 ft altitude and *G. palmata* at 6000–6500 ft altitude.

TABLE 1. SELECTED CHARACTERISTICS OF *Gleichenia bifida*, *G.* × *leonis*, AND *G. palmata*.

Character	*G. bifida*	*G.* × *leonis*	*G. palmata*
Rhizome habit	totally hypogeous	partially epigeous	partially epigeous
Rhizome cross-section	semicircular	semicircular	flattened
Rhizome scales	few	many	many
Primary rachis length	<50 cm	<50 cm	>50 cm
Primary branch length and branching	2.5 & 7 cm, unequal	4–5 cm, equal	3.5–6 cm, equal
Secondary branch length	<5 cm	>5 cm	>5 cm
Quaternary branches	absent	present	present
Laminae beneath	glaucous	not glaucous	not glaucous
Soral paraphyses	present	present	absent
Sporangia position	inframedial	inframedial	medial
Spores	normal	abortive	normal

Local differences in altitude and in habitat may account for the lack of hybrids, although the altitudinal ranges of the parents as a whole overlap greatly. In general, *G. bifida* grows at lower elevations than does *G. palmata*. *Gleichenia bifida* is more a pioneer species, often occuring on raw clay river and road banks, whereas *G. palmata* is commonly recorded from the edges of forests and along trails and ridge tops.

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Publication of the Ferns and Fern-allies in the "Primitiae Florae Costaricensis"

DAVID B. LELLINGER*,[1]

In October 1887 Henri Pittier de Fabrega emigrated from his native Switzerland to Costa Rica. There he founded the Instituto Fisico-Geográfico Nacional de Costa Rica in 1889. He continued to direct this institute until 1903.[2] His collections, along with those of Carlos Wercklé, Pablo Biolley, and Adolfo Tonduz, were among the first large plant collections to be made in Costa Rica, and are now preserved in the Herbario Nacional of the Museo Nacional de Costa Rica in San José.

Pittier, who was a member of several major European scientific societies, including the Société Royale de Botanique de Belgique, desired to publish on the large and interesting Costa Rican flora that he and his associates were collecting so assiduously. For this purpose he enlisted the aid of a number of European taxonomic specialists. Their contributions, each devoted to a single group or family of plants, generally were published in European journals and then reprinted by the Jardin Botanique de l'Etat, Bruxelles, as fascicles of the "Primitiae Florae Costaricensis."

In the beginning of the "Primitiae" (1891), Th. A. Durand, of the Jardin Botanique de l'Etat and its Director from 1902 to 1912 (Morton, 1971, p. 65), shared the general editorship with Pittier. As the series continued, some of the contributors died or withdrew and were replaced by others, which led to changing places of publication and deposition of the holotypes.

As part of my own study of the Pteridophyta of Costa Rica, Panama, and the Chocó, it has been necessary to determine the publication dates and the publishing authors of the various parts of the "Primitiae" that deal with Pteridophyta. Also, it is helpful to know in which institutions the holotype or syntype specimens of species described in the "Primitiae" have been deposited.

The Pteridophyta were published in five parts. The first was by J.-E. Bommer (1829–1895), pteridologist at the Jardin Botanique in Bruxelles, and by H. Christ (1833–1933), of Basel, Switzerland. Bommer died before the first part of Pteridophyta was published, although he is indicated as a coauthor. Probably he was more deeply involved with the publication of some new species in a separate article titled "Filices Novae" in the "Bulletin de l'Herbier Boissier," which antedated publication of the first Pteridophyta fascicle of the "Primitiae" (see

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[1] I am indebted to Sr. Luis Diego Gómez P., of the Museo Nacional de Costa Rica, to Mr. Robert G. Stolze, of the Field Museum, to Dr. John D. Dwyer, of the Missouri Botanical Garden, and to Dr. André Lawalrée, of the Jardin Botanique National de Belgique, for their helpful comments and suggestions.

[2] For an account of Pittier's life and botanical collecting in Panama, see Dwyer (1974). Dwyer (*in litt.*) said Jorge León had pointed out to him that, contrary to his article in "Taxon," Pittier did marry. His wife was from Panama, and her family name was Fabrega.

TABLE 1. PUBLICATION OF THE "PRIMITIAE" FASCICLES CONTAINING FERNS AND FERN-ALLIES

Authors	*Title*	*Original Publication*	*Reprint Publication*	*Types*
Bommer or Christ in Dur. & Pitt.	Filices	Bull. Soc. Roy. Bot. Belg. **35**: Mém. 167–249. 1896[1] 250–252. 253–255.	Prim. Fl. Costar. **1**(3): 97–179. 1897. 180–182. 183–185.	BR
Christ in Pitt.	Filices 2d Mém.	Prim. Fl. Costar. **3**(1): 1–47. 1901. 49–51. 53–57. 59–62. 63–65. 67. 69.		BR or P
Christ	Filices & Lycopodiaceae III	Bull. Herb. Boiss. II, **4**: 936–951. 1904. 957–972. 1089–1104. Bull. Herb. Boiss. II, **5**: 1–16. 1905. 248–260.	Prim. Fl. Costar. **3**: 1–16. 1905. 17–32. 33–48. 49–64. 65–77.	P
Christ	Filices IV	Bull. Herb. Boiss. II, **6**: 45–58. 1906. 159–172. 177–192. 279–288.	Prim. Fl. Costar. **3**: 1–14. 1906. 15–28. 29–44. 45–54.	P
Christ	Filices V	Bull. Herb. Boiss. II, **7**: 257–274. 1907. 585–586. Bull. Soc. Bot. Gen. II, **1**: 216–236. 1909.	Prim. Fl. Costar. **3**: 61–78. 1909. "79–80."[2] 81–101.	P

[1]The following names indicated in this publication as new were in fact published earlier by Bommer & Christ in the Bull. Herb. Boiss. **4**: 657–663. Oct 1896, on the pages indicated: *Aspidium conterminum* (p. 659), *A. prominulum* (p. 659), *Asplenium ceratolepis* (p. 658), *Gleichenia retroflexa* (p. 657), *Hymenophyllum durandii* (p. 657), *Polypodium costaricense* (p. 660), *P. cyclocolpon* (p. 659), *P. flagellare* (p. 660), *P. myriolepis* (p. 661), *P. rosulatum* (p. 662), *P. thyssanolepis* var. *bipinnatifidum* (p. 661), and *Pteris mollis* (p. 658).
[2]The reprint is paged (1) and (2). Pages numbers "79–80" are inferred from the preceeding and following parts.

Table 1, footnote 1), than he was with the "Primitiae" fascicle itself, which had additions made to it, apparently solely by Christ.

Durand withdrew from the general editorship at the close of volume I of the "Primitiae," leaving Pittier to carry on alone. Christ continued his publication of the Pteridophyta. Pittier left Costa Rica in 1904, after publishing fascicle 1 of volume III, and Christ alone published the last three parts of Pteridophyta as journal articles, with specially paged reprints, as had been Pittier's custom.

The original articles and the "Primitiae" reprints[3] each have both the original journal pagination and continuous "Primitiae" pagination. In all but the second fascicle of Pteridophyta, which bears only the "Primitiae" pagination, the "Primitiae" pagination is in parentheses and the original journal pagination is not. In general, the Pteridophyta fascicles each originally appeared in several parts extending over a period of months or years.

Table 1 summarizes the publication data. I would like to mention several important points to show my reasons for adopting certain data in the table.

The "Bulletin de la Société Royale de Botanique de Belgique" appeared each year in two parts. Usually each had first the "Mémoires," containing scientific papers, and second the "Comptes rendus des séances," containing a record of the Society's monthly meetings, which often mention what was to be published in the succeeding "Mémoires." Tournay (1962, p. 36) dates the first "Mémoire" of volume 35 as 17 November 1896. His paper is invaluable to anyone wishing to understand the complexities of publication that have occurred during the long history of the "Bulletin."

Fascicle 1 of volume III of the "Primitiae," titled "Filices 2d Mémoire," appeared in 1901, as the outside of the wrapper indicates, not in 1896 or 1898. The notice on the inside of the wrapper, "Extrait des 'Anales del Instituto Fisico-Geográfico Nacional'.—t. IX. 1896" is in error. Gómez (*in. litt.*) says that the ferns and fern-allies were not published in volume 9 of the "Anales" and that this volume appeared in 1898, not in 1896. It would be possible to construe this fascicle as an addendum to volume 9 of the "Anales" published in 1901, but it is paged separately from the "Anales" and bears only the "Primitiae" pagination. In addition, Christensen (1905) cites the place of publication for new taxa published in this fascicle as "Prim. Fl. Costar. 3(1). 1901." It seems preferable to continue this usage.

The reprinted Pteridophyta fascicles III, IV, and V are headed "Extrait du *Bulletin de l'Herbier Boissier . . .*" and have had their pages rearranged to fill up the space between the parts as originally published. Therefore, it is probable that each of these "Primitiae" reprints was issued as a whole after its last part appeared in the original journal. If this is true, then the "Primitiae" fascicle can be dated no earlier than the date of its last part, as I have indicated in *Table 1*.

The holotypes or syntypes of Pteridophyta described in the "Primitiae" are

[3] Gómez (*in litt.*) points out that in addition to the original journal publication and the doubly paged and re-arranged reprints, there exists a compilation of the "Primitiae" fascicles translated into Spanish that was published by the Instituto Fisico-Geográfico de Costa Rica. This publication made the "Primitiae" readily available and understandable to the people of Costa Rica.

deposited mainly in Bruxelles or in Paris, as indicated in *Table 1*, with the exception of a few specimens that are in the Museo Nacional in San José. After Bommer's death in 1895, Durand sent the pteridophytes arriving from Costa Rica on loan to Christ, who had permission to keep the duplicates (Lawalrée, *in litt.*). Later on, Christ received the collections in bulk directly from Pittier. The two men had been companions in the Schweizerischen Botanischen Gesellschaft (Gómez, *in litt.*). From these collections Christ normally put the holotype or one or more syntypes in his own herbarium, which later became part of the general collection at Paris. Since the specimens are marked "Hb. Christ, Bâle," one can refer to their place of deposition as "P-Hb. Christ." Types of the names that Christ published in the 1901 portion of the "Primitiae" seem to be divided about equally between Bruxelles and Paris, perhaps because his arrangement with Bruxelles concerning the disposition of the types was not clearly formulated at that time. At any rate, each of these cases needs to be investigated. Lectotypes chosen by later authors do not necessarily conform with the above.

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TOURNAY, R. 1962. Notice sur le bulletin de la Société Royale de Botanique de Belgique. Bull. Soc. Roy. Bot. Belg. **95**: 25–39.

Chromosomes of the Male Fern from the Western United States

ELIZABETH ANN REISENDER*,[1]

Dryopteris filix-mas (L.) Schott, the Male Fern, has been shown to represent a species-complex of more or less similar plants. All are fairly large ferns with broad, pale-scaly, tapering blades, deeply pinnatifid pinnae, and large and indusiate sori. In North America the Male Fern occurs mainly in woodlands, often on shaded rocky slopes. It is relatively rare and sporadic. In the east it ranges from Newfoundland through Quebec and eastern Canada southward to northwestern Vermont and northern Michigan. Western populations of this fern (or a fern closely related to it) are separated from the eastern populations by a very large gap in the Great Plains. Reports from the Cascade Mountains of Washington, the Blue Mountains of Oregon, Zion National Park in Utah, western South Dakota, westernmost Oklahoma, and Jeff Davis County, Texas, as well as far western occurrences from British Columbia to the San Bernardino Mountains of California indicate that the western taxon is widely distributed. The considerable break in range between the eastern and western plants has led to the idea that the western *D. filix-mas* may actually be different taxonomically from the eastern. Edgar T. Wherry (1961, p. 114), for example, states that another taxon "commonly treated under the same name but believed to be distinct, is widespread in the w. mts."

The cytotaxonomic problems of the genus *Dryopteris* were first studied extensively in Britain by I. Manton (1950, pp. 44–62). The genus presents an imposing evolutionary problem because of its tendency to hybridize and to produce numerous variations in morphology, ecology, and distribution. Manton determined a basic chromosome number of $x=41$ for the genus. Although *D. filix-mas* was originally reported to be tetraploid ($n=82$, $2n=164$), cytological observations of artificially made hybrids between the very similar *D. abbreviata* (a diploid) and *D. filix-mas* indicated that the diploid was probably one of the ancestors of the tetraploid. The other ancestral diploid was unknown at the time. Fraser-Jenkins and Corley (1972) recently proposed that the other ancestor is the plant known as *D. caucasica*; the morphology and the characteristics of the hybrids of *D. caucasica* support this proposal. Although at present the two diploid taxa do not overlap in range in Europe, it is conceivable that they once did during an earlier geological period, and it was at that time that the tetraploid originated by hybridization.

Previous chromosome observations of *D. filix-mas* in North America have been from the northeastern United States and eastern Canada. The first report was by Wagner and Hagenah (1962); subsequent studies in the eastern United States and Canada have supported $n=82$ as the diploid chromosome number. The present paper gives the first report for any western member of the *D. filix-mas*

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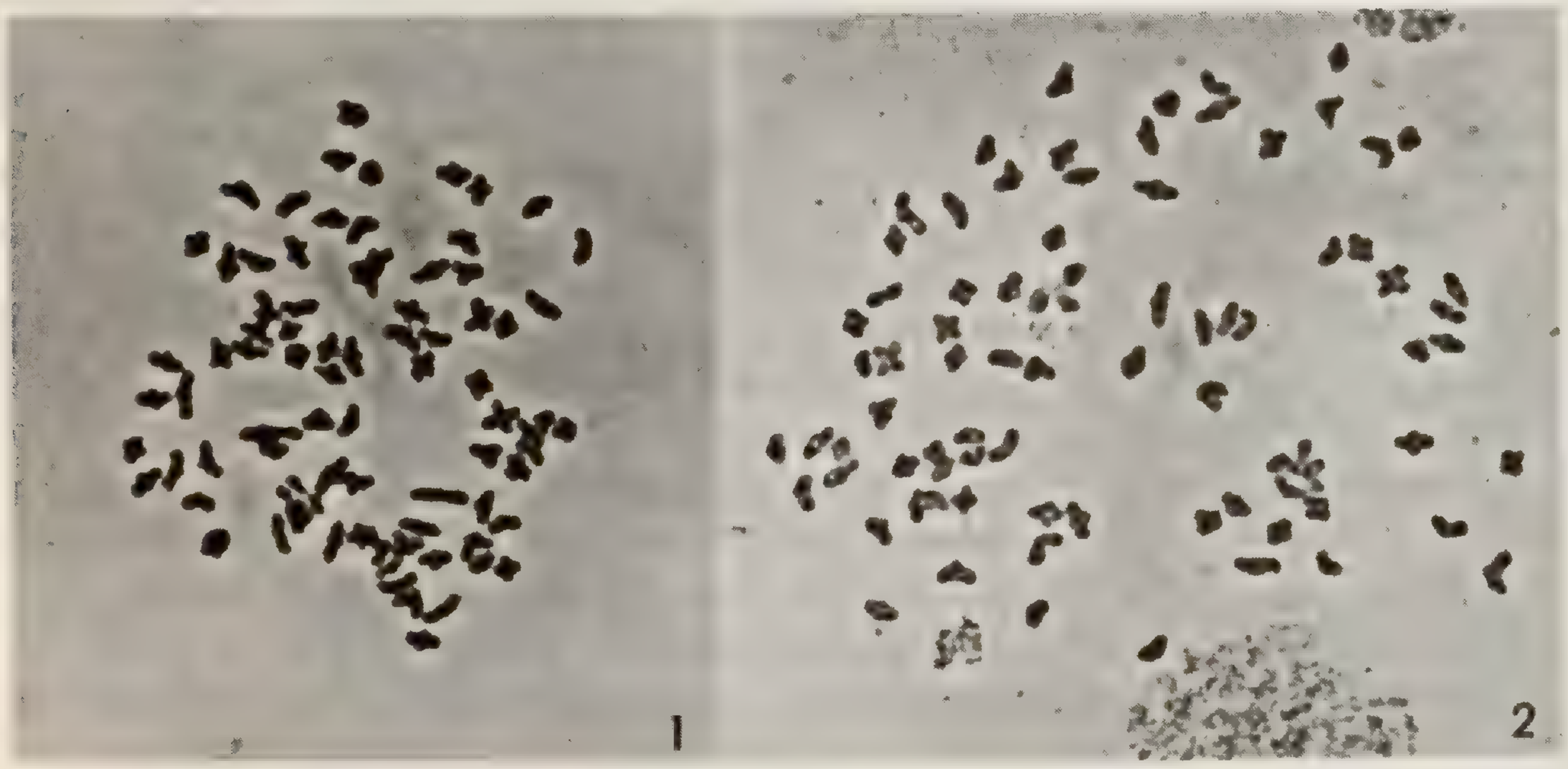
[1]I am indebted to Dr. Florence S. Wagner for help in certain parts of this study. This work was completed under NSF Grant GB-30918X, "The Evolutionary Characters of the Ferns."

complex. The plant was taken on 22 August 1969 from a rocky shaded slope along Perry Creek in Chelan County, Washington (*Wagner 69256*, MICH). Subsequently it was grown at the University of Michigan, where the chromosomes were obtained. Meiotic configurations show $n=82$ pairs; no distinctions were found between these and figures obtained from plants in eastern North America. *Figures 1* and *2* show squashes of spore mother cells to illustrate the perfect pairing of the chromosomes.



FIGS. 1–2. Meiotic chromosomes of western *Dryopteris filix-mas* stained and squashed with aceto-carmine, showing 82 pairs of chromosomes (*Wagner 69256*, MICH).

Because the results of my study agree with those previously made on eastern populations, there is support for the idea that eastern and western *D. filix-mas* are actually conspecific, in spite of suggestions that they might represent separate taxa. Not only the cytology, but also the morphology tends to support this view.

The recent discovery by Fraser-Jenkins and Corley that *D. caucasica* is a probable ancestral diploid answers some of our questions as to the origin of *D. filix-mas*. It is probable that *D. filix-mas* originated as an interspecific hybrid in Europe and spread to North America. With the information presented here, it seems conceivable that an original introduction spread across North America, and that, unlike the situation in Europe, the New World Male Fern complex comprises a single, uniform, tetraploid species.

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A Revised Classification of Thelypteris Subgenus Amauropelta

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Thelypteris subgenus *Amauropelta* is a highly natural, probably monophyletic group occurring principally in the New World tropics and subtropics. The number of species is large; Christensen (1907, 1913) recognized about 120, and 55 have been described since then. Many undescribed species remain. The size of the subgenus in terms of both the number of "good" species (perhaps 200) and the number of basionyms assignable to the subgenus (ca. 400) makes it desirable that an infrasubgeneric classification be achieved before a revision of closely related species groups is undertaken and before additional species are described.

Christensen made no attempt to subdivide subg. *Amauropelta* (his *Dryopteris* subg. *Lastrea*), but he did recognize small groups of closely related species. As a result of my studies, I feel that the species fall naturally into nine more or less distinct groups, to be given the rank of section. There are relatively few basionyms that must remain unplaced, either because of intermediacy between sections or because type material has not yet been seen. I have attempted to account for all basionyms (based on New World specimens) that should be included within the circumscription of subg. *Amauropelta*. No doubt a few have been missed, especially infraspecific names. The search has been difficult because species have been described under so many different genera and because of the huge number of species in *Thelypteris* s.l. (perhaps 1000). An asterisk following a name in the enumeration of basionyms indicates that I have seen type material.

I thank R. E. Holttum for helping with the Latin diagnoses and curators of the following herbaria for loan of types: A, B, DS, F, GH, HB, K, M, R, SI, S, S-PA, US.

TAXONOMIC CHARACTERS

Rhizome.—Rhizome habit is preponderantly suberect to erect in all sections except sect. *Adenophyllum*, where it is usually decumbent. Creeping rhizomes occur in a few Andean species of sect. *Lepidoneuron* [e.g., *Thelypteris caucaensis* (Hieron.) Alston], and in a few rather aberrant species of sect. *Amauropelta* [*T. firma* (Bak. ex Jenm.) Proctor and allies]. I am uncertain which condition (Rhizome decumbent or erect) is ancestral for the subgenus. Probably evolution has proceeded in both directions within the subgenus and within individual sections.

Stipes.—The bases of stipes, and even entire croziers, of several species groups, i.e., sect. *Phacelothrix*, sect. *Blennocaulon*, and sect. *Amauropelta*, are coated with mucilage. Full development of this layer depends in part on microhabitat: extremely wet or humid conditions seem to favor greater production of mucilage. Microscopic examination of stipes coated with mucilage shows that this layer is the result of secretion by dense, glandular trichomes (Hennipman, 1968; Smith, unpublished).

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Aerophores.—The presence of aerophores at the bases of pinnae and sometimes pinnules is positively correlated with the production of mucilage. Aerophores occur in all species of sect. *Phacelothrix*, where they may be as much as 5 mm long, and in nearly all species of sections *Blennocaulon* and *Amauropelta*. They also occur in a few species of sect. *Uncinella* [*T. diplazioides* (Desv.) Proctor and allies] and sect. *Lepidoneuron* [*Polypodium crossii* Baker]. Aerophores are seemingly absent in species belonging to sections *Apelta*, *Adenophyllum*, and *Blepharitheca*.

Buds.—Many, but not all, species in sect. *Uncinella* produce buds in the axils of upper pinnae. While still attached to the parent plant, these bulblets may remain undeveloped, or they may develop only upon contact with the ground, or they may produce small plantlets. The presence or absence of such buds is usually constant for a given species. Bulblets are unknown in other sections of subg. *Amauropelta*, but do occur in another distantly related subgenus, *Goniopteris*.

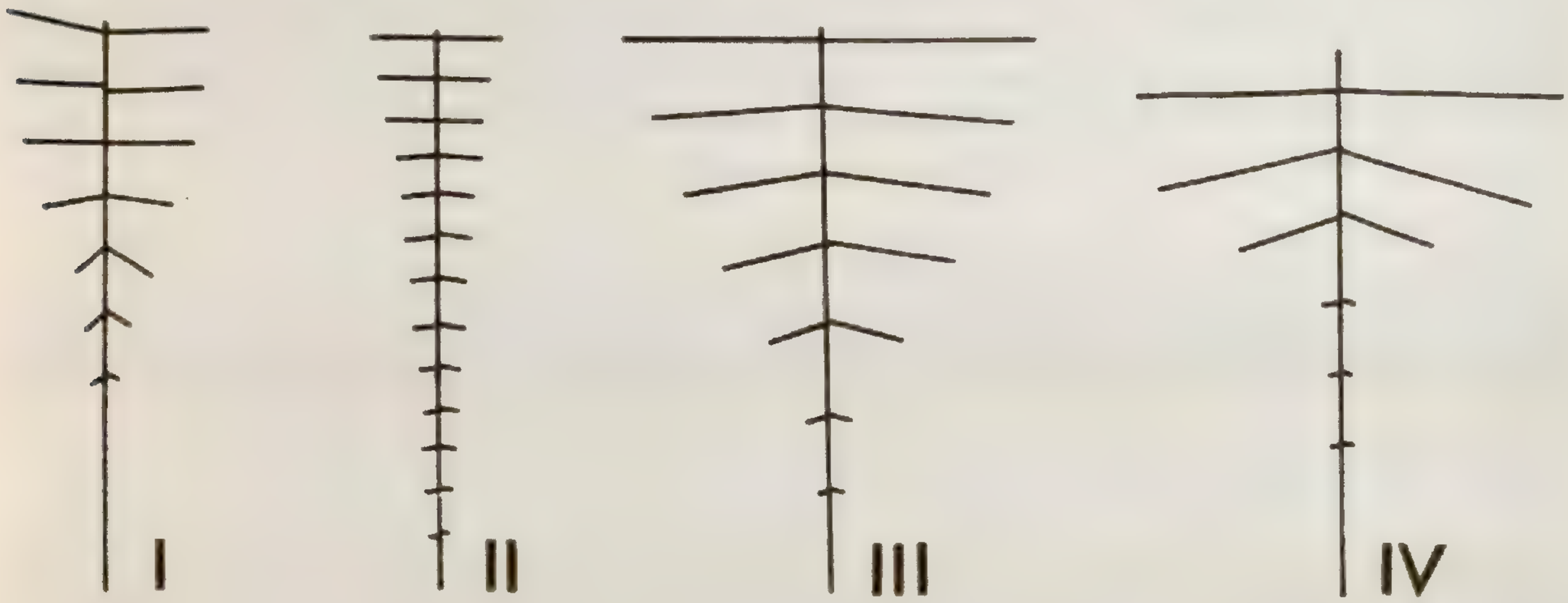

FIG. 1. Blade shapes in *Thelypteris* subg. *Amauropelta* (from Christensen, 1907).

Blade shape.—Christensen (1907) recognized five blade types, four of which I find useful for descriptive purposes (*Fig. 1*). Species belonging to sections *Lepidoneuron* and *Phacelothrix* consistently have blade type IV, with abruptly reduced lower pinnae and several, small, abortive glanduliform pinnae that are often overlooked. Most species of sect. *Uncinella* have blade type I, with 3–6 gradually reduced pinnae, the lowermost auriculiform. The species of sect. *Amauropelta* are preponderantly blade type II, but there is a line of evolution within the section culminating in a blade with few or even no reduced pinnae (*reducta*, *firma*). In subg. *Amauropelta*, the absence of reduced pinnae is, I believe, derived. Sections *Adenophyllum* and *Blennocaulon* contain species with blade type III.

Blade texture.—Blade texture is subject to great environmental influence, but nevertheless is of use in delimiting large groups of species. Section *Apelta* and species in sect. *Uncinella* related to *T. oligocarpa* (Willd.) Ching are thin-textured. Those species of sect. *Lepidoneuron* allied to *T. rudis* (Kunze) Proctor

generally have a very thick, even coriaceous, lamina. The species of sect. *Blennocaulon* have a subsucculent blade, with slightly impressed and darkened veins.

Sorus.—There is a tendency for sori to be somewhat elongate along the veins in several species of sect. *Uncinella* [e.g., *T. linkiana* (Presl) Tryon and allies]. This condition is certainly derived evolutionarily from species with round sori. Many species in sect. *Lepidoneuron* have slightly oblong sori. Sorus position varies greatly within most sections, but is consistently submarginal in species of sect. *Uncinella* related to *T. oligocarpa* and in *T. cheilanthoides* (sect. *Blennocaulon*).

Indusium.—The generalized and probably ancestral condition in subg. *Amauropelta* is indusiate. The indusium has been lost along several presumably separate evolutionary lines, however. Indusia are consistently absent in sect. *Apelta*, sect. *Blepharitheca*, and sect. *Lepidoneuron*, and absent in a few species of sect. *Blennocaulon* and sect. *Uncinella* [e.g., *T. linkiana*]. In the two last-named cases, the exindusiate species are clearly derived from indusiate ones. A reduced indusium has resulted in many species being described falsely as exindusiate.

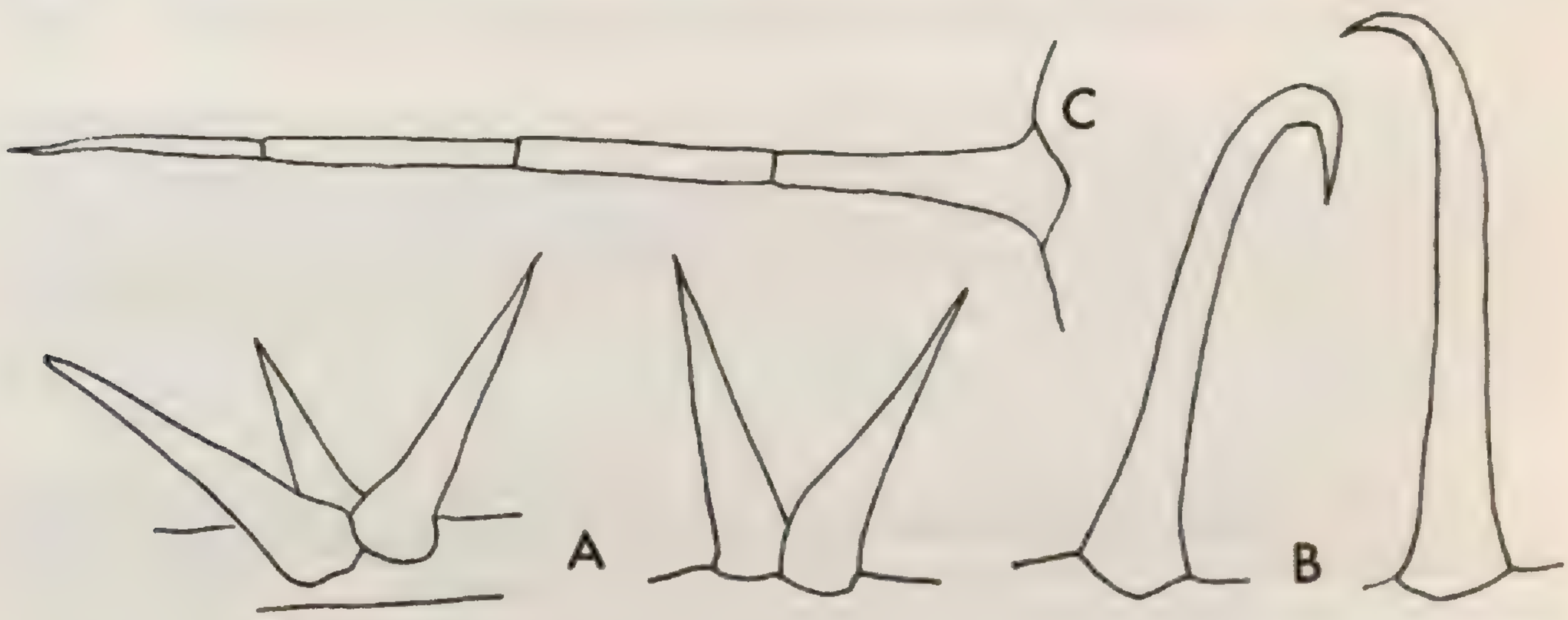

FIG. 2. Hair types in *Thelypteris* subg. *Amauropelta*. A, Fasciculate hairs in *Thelypteris thomsonii* (sect. *Phacelothrix*). B, Uncinate hairs in *Thelypteris melanochlaena* (sect. *Uncinella*). C, Septate hairs in *Thelypteris cheilanthoides* (sect. *Blennocaulon*).

Of the indusiate groups, the species of sect. *Pachyrachis* and most species of sect. *Blennocaulon* have the largest and most persistent indusia.

Indusial color can be important in distinguishing certain species groups. The species of sect. *Uncinella* allied to *T. diplazioides* have greenish indusia. A small group of species in sect. *Amauropelta* show dark, reddish-brown indusia (*sanctiformis, cooleyi, cornuta, brachypoda*).

Sporangia.—Paraphyses are known only from the sporangial walls of several species of sect. *Blepharitheca*, *T. firma* (sect. *Amauropelta*), *Dryopteris heineri* C. Chr., and *D. peruviana* Rosenst. (sect. *Lepidoneuron*), and in a few species of sect. *Adenophyllum* [e.g., *T. subandina*]. Sporangial setae are probably independently derived in all four sections.

Spores.—Wood's (1973) survey of spores in the Thelypteridaceae provides convincing evidence for the homogeneity of subg. *Amauropelta*. At the light microscope level, the spores appear to have a uniform, granular surface. Under the scanning electron microscope, the surface is a highly anastomosing, uniform reticulum which is very distinct from most other Thelypteridaceae. There seems to be very little variability within the subgenus, although Wood reports that *T. firma* has spores with only a partial reticulum and *T. aspidioides* has spores with a spiny reticulum. Both of these species, although somewhat atypical, are good members of *Amauropelta* on other morphological grounds.

Hairs.—Hair types are illustrated in *Fig. 2*. Again, convergent evolution has obscured the more basic pattern of divergent evolution. Septate hairs occur in nearly all species belonging to sect. *Blennocaulon*. But they occur also in a few species of other sections, as in *T. balbisii* (Spreng.) Ching (sect. *Amauropelta*) and in the species of sect. *Adenophyllum* related to *T. argentina* (Hieron.) Abbiatti.

The uncinate (hamate) hairs of sect. *Uncinella* (*Fig. 2B*) are nearly always diagnostic for the section, but a few such hairs can occasionally be found in some specimens of *T. rudis* (sect. *Lepidoneuron*) and *T. rivularioides* (sect. *Adenophyllum*).

The peculiar, fasciculate hairs of sect. *Phacelothrix* (*Fig. 2A*) are approached by the hairs of *T. phacelothrix* (Rosenst.) Tryon (sect. *Lepidoneuron*). This species is possibly an evolutionary link to sect. *Phacelothrix*.

Hairs of subg. *Amauropelta* are generally spreading, but in sect. *Lepidoneuron* they are usually antrorse on the costae below. Other hair characters, such as length, stiffness, and color are certainly important in distinguishing species, and may be important in distinguishing groups of species.

Glands.—At least three kinds of glands or glandular hairs occur in subg. *Amauropelta*: (1) sessile, hemispherical, red glands are common in many species of sect. *Amauropelta*; (2) short-stipitate, light yellowish glands are found in most species of sect. *Adenophyllum*; and (3) clavate, deep red glands are present in a small group of species of sect. *Adenophyllum* related to *T. argentina*. The absence of glands is nearly always diagnostic for sections *Uncinella, Apelta,* and *Lepidoneuron*.

TAXONOMIC TREATMENT

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Thelypteris subg. Amauropelta (Kunze) A. Reid Smith, Amer. Fern J. 63: 121. 1973.

Amauropelta Kunze, Farnkr. **1:** 86, 109. 1843. TYPE: *Amauropelta breutelii* Kunze [=*Thelypteris limbata* (Swartz) Proctor].

Oochlamys Fée, Gen. Fil. 297. 1852. TYPE: *Oochlamys rivoirei* Fée [= *Thelypteris opposita* (Vahl) Ching]. L 24058

Dryopteris subg. *Lastrea sensu* C. Chr. Biol. Arb. tilg. Eug. Warming 79. 1911, and *sensu* C. Chr. K. Danske Vidensk. Selsk. VII, **10:** 55–282. 1913.

Thelypteris subg. *Lastrea sensu* Alston, J. Wash. Acad. Sci. **48**: 232. 1958, and *sensu* Morton, Amer. Fern J. **53**: 153. 1963.

Rhizomes suberect to erect, occasionally decumbent; blades pinnate-pinnatifid (rarely pinnate or decompound), with the lowermost pinnae reduced, sometimes nearly to the rhizome; aerophores present at the bases of pinnae, or absent; veins usually simple, occasionally furcate, meeting the margin of the segments, the lowermost veins of each segment running to the margin above the sinus; sori round to occasionally somewhat elongate, medial to submarginal on the veins, furnished with large to small indusia or indusia absent; sporoderm evenly granular (light microscope), finely reticulate (scanning electron microscope); $x=29$.

About 200 species, found mostly at middle to higher elevations on the margins of rain forests, along trails, wet roadside embankments, and the margins of streams, in tropical and subtropical America (Mexico, Florida, the Antilles, Central America, and South America to northern Argentina and Chile), with one species in Hawaii and one or a few in Africa, Madagascar, and the Mascarene Islands.

Some epithets have not yet been transferred to *Thelypteris*, and others need not be. I have cited names as basionyms or as epithets alone in some cases where the names are correct in *Thelypteris* but the combinations may or may not have been made.

KEY TO THE SECTIONS OF THELYPTERIS SUBG. AMAUROPELTA

1. Indusia present.
   2. Rhizomes usually creeping, suberect in a few species; laminae and axes with short-stipitate, light yellowish glands; veins often furcate; aerophores absent ..... 1. *Adenophyllum*
   2. Rhizomes suberect to erect; laminae with sessile glands or eglandular; veins unbranched; aerophores present or absent.
      3. Hairs on rachises and costae fasciculate; prominent aerophores up to 5 mm long at base of costae and usually costules; blades abruptly reduced below (Type IV) ..... 2. *Phacelothrix*
      3. Hairs on rachises and costae not fasciculate, ± evenly distributed; aerophores present or absent, never at bases of costules.
         4. Laminae with uncinate hairs; sori often submarginal, furnished with a very small indusium; blades with ca. 3–6 pairs of gradually reduced pinnae (Type I); blades and indusia without glands ..... 3. *Uncinella*
         4. Laminae with straight hairs or glabrous; sori medial to submarginal, the indusia easily visible; blades and often indusia glandular.
            5. Laminae usually gradually tapering nearly to the rhizome, with many pairs of reduced pinnae (Type II); laminae and axes pubescent, the hairs unicellular ..... 4. *Amauropelta*
            5. Laminae with usually fewer than 8 pairs of gradually reduced pinnae (Type III); laminae and axes glabrous or pubescent with septate hairs.
               6. Axes pubescent with septate hairs; veins slightly sunken below, often darkened; sori submarginal ..... 5. *Blennocaulon*
               6. Axes without hairs; veins flush or slightly raised; sori medial ..... 6. *Pachyrachis*

1. Indusia absent.
   7. Scales present on costae below, these sometimes clathrate or subclathrate; blades rather abruptly reduced below, with several abortive or auriculiform pinnae (Type IV) ..... 7. *Lepidoneuron*
   7. Scales absent on costae below; blades gradually reduced.
      8. Laminae and axes with uncinate hairs ..... 3. *Uncinella*
      8. Laminae and axes with straight hairs.
         9. Rachises and costae with dense, minute pubescence, the hairs less than 0.1 mm long; stipes and rachises darkened; sporangia glabrous or setose ..... 8. *Blepharitheca*
         9. Rachises and costae sparsely pubescent to glabrous; stipes and rachises stramineous; sporangia glabrous ..... 9. *Apelta*

1. Thelypteris sect. Adenophyllum A. Reid Smith, sect. nov.

Rhizomata repentia vel erecta; laminae deorsum sensim reductae (Typus II), pinnis infimis auriculiformibus, distantibus; bases pinnarum aerophoris destitutae; costae, venae et laminae glandulis stipitatis flavidis praeditae, paleis destitutae; indusia praesentia, saepe magna.

TYPE: *Aspidium rivularioides* Fée [≡ *Thelypteris rivularioides* (Fée) Abbiatti].

Perhaps 25 species, in southern Brazil, northern Argentina, Paraguay, Uruguay, Bolivia to Colombia, Venezuela, and north to southern Mexico. The only species occurring in North America is *T. pilosula* (Mett.) Tryon, from southern Mexico to Peru.

Aspidium achalense Hieron.*, *Aspidium arechavaletae* Hieron., *Aspidium argentinum* Hieron., *Thelypteris burkartii* Abbiatti*, *Polypodium camporum* Lindman, *Aspidium galanderi* Hieron.*, *Dryopteris glanduloso-lanosa* C. Chr.*, *Dryopteris hassleri* Christ*, *Dryopteris janeirensis* Rosenst.*, *Nephrodium juergensii* Rosenst.*, *Dryopteris juergensii* (Rosenst.) C. Chr. var. *hirsutula* Rosenst.*, *Aspidium lorentzii* Hieron.*, *Thelypteris minensis* Abbiatti, *Dryopteris mosenii* C. Chr.*, *Dryopteris neglecta* Brade & C. Chr.*, *Aspidium oligocarpum* (Willd.) H.B.K. var. *crassistipitatum* Hieron.*, *Dryopteris organensis* Rosenst.*, *Thelypteris pilosissima* Morton*, *Aspidium pilosulum* Mett.*, *Thelypteris platensis* Abbiatti*, *Aspidium pseudomontanum* Hieron., *Nephrodium pseudothelypteris* Rosenst.*, *Dryopteris rimbachii* Rosenst.*, *Aspidium rivularioides* Fée*, *Dryopteris rivularioides* (Fée) Rosenst. var. *crenata* Rosenst.*, *Dryopteris rivularioides* (Fée) Rosenst. var. *umbratica* Rosenst.*, *Dryopteris rojasii* Christ*, *Dryopteris rosei* Maxon*, *Dryopteris santae-catharinae* Rosenst.*, *Dryopteris scariosa* Rosenst.*, *Aspidium siambonensis* Hieron.*, *Dryopteris subandina* C. Chr. & Rosenst., *Dryopteris subandina* f. *minor* C. Chr. & Rosenst.*, *Dryopteris vattuonei* Hicken*.

This is perhaps the most heterogeneous of any of the sections that I recognize, but I believe that the species included within it are all more closely related to each other than to members of any of the other sections. Three elements can be discerned: (1) a group of very poorly circumscribed species with long-creeping rhizomes, occurring in southern Brazil, northern Argentina, Uruguay, and Paraguay (*achalense, hassleri, janeirensis, juergensii, mosenii, neglecta, platensis, rivularioides, rojasii, santae-catharinae, scariosa, siambonense, vattuonei*); (2) species allied to *T. argentina* (Hieron.) Abbiatti, with suberect rhizomes, stramineous stipes with blackened bases, and deep-red glands at the bases of costules and sometimes along the costules, distributed primarily in northwestern Argentina, Chile, Bolivia, and Peru (*argentina, burkartii, galanderi, glanduloso-lanosa, lorentzii*); and (3) species allied to *T. pilosula*, with long, dense, stiff, spreading hairs covering the rachis and costae, and an erect rhizome (*pilosissima, pilosulum, rimbachii*). The two last-named groups are connected through such species as *subandina*.

2. Thelypteris sect. Phacelothrix A. Reid Smith, sect. nov.

Rhizomata crassa, erecta; frondes volutae mucosae; pinnae versus basin laminarum abrupte reductae (Typus IV), pinnis infimis glandiformibus; aerophora usque 5 mm longa e basibus costarum costularumque exorientia; costae subtus paleis destitutae; laminae subtus (etiam venae) pilis fasciculatis glandulisque sessilibus rubris vestitae; indusia parva.

TYPE: *Polypodium thomsonii* Jenm. [≡ *Thelypteris thomsonii* (Jenm.) Proctor].

About 5 species, in montane cloud forests, at middle to higher elevations, from Hispaniola, Jamaica, southern Mexico (Oaxaca, Chiapas), Central America, and

Colombia to Bolivia.

Dryopteris andina Morton, *Dryopteris boliviensis* Morton, *Nephrodium cañadasii* Sod., *Nephrodium macradenium* Sod., *Dryopteris stubelii* Hieron., *Polypodium thomsonii* Jenm.

The species belonging to sect. *Phacelothrix* were formerly included in subg. *Glaphyropteris* by Christensen (1913) and in sect. *Glaphyropteris* by Morton (1938). However, *Glaphyropteris*, in my opinion, is an unnatural group, an idea first suggested to me a few years ago by R. E. Holttum. The type of *Glaphyropteris* [*T. decussata* (L.) Proctor] and its allies [*T. mapirensis* (Rosenst.) Alston, *T. comosa* (Morton) Morton, *T. polyphlebia* (C. Chr.) Morton, *T. brasiliensis* (C. Chr.) Morton, and *T. tatei* (Maxon & Morton) Morton] are all characterized by non-fasciculate septate hairs, the absence of reduced proximal pinnae, very close veins, and exindusiate sori. These species are all found at low to middle elevations, usually below 2000 m. *Thelypteris decussata* is the only species from which a chromosome count has been obtained, reported by Sorsa (in Fabbri, 1965) as $n=72$.

The remaining species in *Glaphyropteris sensu* Morton I include in sect. *Phacelothrix*; these are all characterized by having fasciculate, non-septate hairs, abruptly reduced basal pinnae, veins further apart, and indusiate sori. All of the species occur at higher elevations, generally above 2000 m. The sole species known chromosomally is *T. thomsonii*, reported by Walker (1966) as $n=58$.

Section *Phacelothrix* seems to me to be most closely related to sect. *Lepidoneuron*, through such species as *T. phacelothrix* (Rosenst.) Tryon, which bears costal scales like those of species of sect. *Lepidoneuron*, but shows a tendency toward the fasciculate hairs of sect. *Phacelothrix*.

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3. Thelypteris sect. Uncinella A. Reid Smith, sect. nov.

Rhizomata erecta vel repentia; laminae basin versus gradatim angustatae, 3–5 (raro pluribus) paribus pinnarum inferiorum reductis (Typus I); axillae pinnarum distalium saepe gemmiferae; costae subtus plerumque paleis destitutae; laminae eglandulosae, subtus (etiam venae) pilis uncinatis, supra pilis appressis vestitae; sori rotundi vel leviter elongati; indusia parva, saepe abscondita, vel nulla.

TYPE: *Polypodium oligocarpum* Willd. [≡ *Thelypteris oligocarpa* (Humb. & Bonpl. ex Willd.) Ching].

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Perhaps 50 species, from the Antilles, southern Mexico (5 sp.) through Central America and South America to Bolivia and southern Brazil. At least one species, *T. bergiana* (Schlecht.) Ching, occurs in Africa.

Ceterach aspidioides Willd., *Dryopteris aspidioides* (Willd.) C. Chr. var. *subhastata* C. Chr., *Gymnogramma asplenioides* Swartz, *Polypodium asplenioides* Swartz, *Aspidium atrorubens* Mett.*, *Dryopteris atrovirens* C. Chr. in Christ*, *Nephrodium brachypus* Sod.*, *Dryopteris columbiana* C. Chr.*, *Nephrodium conforme* Sod.*, *Polypodium consanguineum* Klotzsch*, *Aspidium diplazioides* Moritz ex Mett.*, *Dryopteris diplazioides* (Desv.) Urban var. *brevisora* Rosenst.*, *Gymnogramma diplazioides* Desv., *Dryopteris dominicensis* C. Chr.*, *Phegopteris duchassaigniana* Fée, *Dryopteris dutrai* C. Chr. ex Dutra, *Aspidium fischeri* Mett., *Aspidium funckii* Mett.*, *Dryopteris funckii* (Mett.) Kuntze var. *angustiloba* Hieron., *Dryopteris funckii* var. *obtusa* Hieron., *Dryopteris funckii* var. *strigosa* Hieron., *Phegopteris germaniana* Fée, *Gymnogramma gracilis* Heward [≡ *Grammitis hewardii* Moore], *Gymnogramme gracilis* Heward var. *consimilis* Fée ex Baker, *Phegopteris gracilis* (Heward) Mett. var. *guadalupensis* Fée, *Polypodium heteroclitum* Desv., *Phegopteris hydrophila* Fée, *Polypodium induens* Maxon var. *subdentatum* Bosco, *Dryopteris irenae* Brade, *Aspidium kaul-*

fussii Link*, *Aspidium lasiesthes* Kunze, *Dryopteris leptogrammoides* Rosenst., *Dryopteris lindmanii* C. Chr.*, *Grammitis linkiana* Presl, *Dryopteris lomatosora* Copel.*, *Dryopteris melanochlaena* C. Chr.*, *Dryopteris mollicella* Maxon*, *Dryopteris moritziana* Urban, *Aspidium navarrense* Christ, *Nephrodium nimbatum* Jenm., *Polypodium oligocarpum* Humb. & Bonpl. ex Willd., *Polypodium oligosorum* Klotzsch, *Gymnogramme oppositans* Fée, *Gymnogramme polypodioides* Link, *Aspidium ptarmica* Kunze ex Mett., *Dryopteris ptarmiciformis* C. Chr. & Rosenst.*, *Aspidium pusillum* Mett., *Dryopteris raddii* Rosenst. var. *itatiayensis* Rosenst., *Dryopteris recumbens* Rosenst.*, *Dryopteris recumbens* var. *violacea* Rosenst., *Dryopteris regnelliana* C. Chr., *Polypodium retusum* Swartz [≡ *Dryopteris raddii* Rosenst.], *Dryopteris retusa* (Swartz) C. Chr. f. *denticulata* Rosenst., *Dryopteris rioverdensis* C. Chr.*, *Dryopteris rivulariformis* Rosenst. [≡ *Dryopteris stenophylla* Rosenst., 1908, *non* C. Chr., 1905], *Leptogramme rupestris* Klotzsch*, *Phegopteris rustica* Fée, *Polypodium saxicola* Swartz, *Aspidium scalare* Christ*.

At least three distinct groups of species can be recognized within sect. *Uncinella:* (1) the group of *T. linkiana* (Presl) Tryon, which includes species with exindusiate, often elongate sori, short-stipitate lower pinnae, and less deeply incised pinnae (e.g., *aspidioides, linkiana, ptarmica*); (2) the group of *T. diplazioides* (Moritz ex Mett.) Ching, with more numerous reduced pinnae, more or less prominent aerophores, relatively large indusia that are greenish in several species, more scaly axes culminating in the rather densely scaly costae of *T. funckii* (Mett.) Alston (e.g., *brachypus, diplazioides* Mett., *dominicensis, funckii, rustica*); and (3) the group of *T. oligocarpa*, with deeply cut pinnae, often falcate segments, submarginal sori furnished with minute indusia, and the absence of aerophores. This group contains the bulk of the species in the section. Groups 1 and 2 seem to me to be derived from Group 3.

Section *Uncinella* is evidently most closely related to sect. *Lepidoneuron*, on one hand, and sect. *Adenophyllum* on the other. Nearly all species can be readily placed by the character of uncinate hairs.

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Rhizomata erecta (vel speciebus paucis repentia); stipites perbreves; laminae plerumque basin versus sensim reductae (Typus II), pinnis reductis multis; aerophora parva, manifesta; laminae glandulosae vel eglandulosae, glandulis sessilibus, rubris vel aurantiacis; indusia praesentia, straminea vel brunneola, saepe glandulosa.

TYPE: Same as subg. *Amauropelta*.

Perhaps 50 species, from Florida (1 species), the Antilles, Mexico (4 species) through Central America, and tropical South America from Colombia to Bolivia and southeastern Brazil (1 species).

The center of evolution of the section is in the West Indies, where there are about 20 species, most of them endemic to one or a few islands. The species with red glands have been discussed by Morton (1963); however, not all these species belong in this section.

A single Hawaiian species, *Thelypteris globulifera* (Brack.) Reed, appears to belong in this section. It agrees with Neotropical members in having sessile, red glands, gradually decrescent lamina, relatively large, persistent indusia, and small aerophores. A chromosome count is highly desirable and, if based on 29, would provide nearly conclusive evidence of its New World affinities, in my opinion. According to Holttum (pers. comm.), a few African species may also belong in this section.

Phegopteris adenochrysa Fée, *Dryopteris aequatorialis* Copel.*, *Dryopteris aliena* C. Chr.*, *Nephrodium amphioxypteris* Sod.*, *Lastrea angustata* Presl, *Polypodium balbisii* Spreng., *Nephrodium basiattenuatum* Jenm., *Aspidium berteroanum* Fée, *Nephrodium brachypodum* Bak.*, *Amauropelta breutelii* Kunze, *Nephrodium caribaeum* Jenm.*, *Aspidium coarctatum* Kunze, *Dryopteris coarctata* (Kunze) C. Chr. var. *longipes* C. Chr., *Aspidium consanguineum* Fée, *Aspidium conterminum* Willd., *Thelypteris cooleyi* Proctor*, *Dryopteris cornuta* Maxon*, *Dryopteris crespiana* Bosco, *Aspidium exsudans* Fourn., *Nephrodium firmum* Bak. ex Jenm., *Dryopteris furva* Maxon*, *Aspidium ghiesbreghtii* Fourn., *Aspidium glanduliferum* Karst. ex Klotzsch*, *Dryopteris glutinosa* C. Chr.*, *Polypodium gracilentum* Jenm., *Dryopteris harcourtii* Domin, *Dryopteris hastiloba* C. Chr.*, *Nephrodium jamaicense* Bak. in Jenm., *Lastrea leiboldiana* Presl, *Dryopteris leucothrix* C. Chr.*, *Dryopteris leucothrix* C. Chr. var. *glanduligera* C. Chr. & Rosenst., *Aspidium limbatum* Swartz, *Polypodium litigiosum* Liebm.*, *Nephrodium longicaule* Baker*, *Dryopteris mercurii* A. Braun ex Hieron., *Thelypteris minutula* Morton*, *Thelypteris mortonii* A. Reid Smith*, *Nephrodium nockianum* Jenm., *Dryopteris novaeana* Brade, *Dryopteris opposita* (Vahl) Urban var. *geraensis* C. Chr., *Dryopteris opposita* var. *longissima* C. Chr., *Dryopteris opposita* var. *mettenii* Rosenst., *Dryopteris opposita* (Vahl) Urban var. *pubescens* Hieron., *Polypodium oppositum* Vahl, *Aspidium pachychlamys* Fée, *Nephrodium panamense* Presl, *Dryopteris panamensis* (Presl) C. Chr. var. *gonzalezii* C. Chr., *Dryopteris panamensis* var. *proxima* C. Chr.*, *Aspidium physematioides* Kuhn & Christ in Krug, *Dryopteris piedrensis* C. Chr.*, *Polypodium plumieri* Desv., *Aspidium polyphyllum* Kaulf., *Dryopteris pseudosancta* C. Chr.*, *Thelypteris randallii* Maxon & Morton*, *Dryopteris reducta C. Chr.**, *Polypodium resiniferum* Desv., *Aspidium rigidulum* Mett. ex Kuhn*, *Oochlamys rivoirei* Fée, *Polypodium rivulorum* Raddi, *Dryoptèris sanctiformis* C. Chr.*, *Aspidium sanctoides* Fée, *Acrostichum sanctum* L. [≡ *Lastrea linnaeana* Copel.], *Nephrodium sanctum* (L.) Baker var. *hirtum* Jenm., *Dryopteris sancta* (L.) Kuntze var. *portoricensis* C. Chr., *Dryopteris sancta* var. *strigosa* C. Chr., *Dryopteris sancta* var. *terminalis* C. Chr., *Nephrodium sanctum* (L.) Baker var. *magnum* Jenm., *Phegopteris scalpturoides* Fée*, *Dryopteris scalpturoides* (Fée) C. Chr. var. *subbipinnata* C. Chr.*, *Dryopteris scalpturoides* var. *jamaicensis* C. Chr., *Dryopteris shaferi* Maxon & C. Chr.*, *Nephrodium sherringii* Jenm., *Aspidium sprengelii* Kaulf., *Dryopteris sprengelii* (Kaulf.) Kuntze var. *longipilosa* C. Chr., *Aspidium strigosum* Fée, *Dryopteris struthiopteroides* C. Chr.*, *Phegopteris tenella* Fée, *Dryopteris underwoodiana* Maxon, *Dryopteris vaccanea* Bosco.

I have included several primarily South American species in sect. *Amauropelta;* these differ from the bulk of the Antillean species in having a much smaller number of reduced basal pinnae, darkened (sometimes atropurpureous) stipes and rachises, lamina without bright sessile glands, and in indusia larger, more rotund, glabrous, and dark brown (*brachypodum, cooleyi, cornuta, furva, longicaule,* and *sanctiformis*).

Another natural group, perhaps deserving subsectional recognition, within sect. *Amauropelta* is the group that culminates in *Thelypteris firma* (Bak. ex Jenm.) Proctor. Allied species are *aliena* and *reducta*. This small group is connected to more typical members of sect. *Amauropelta* through such species as *scalpturoides, shaferi,* and *hastiloba*. Character trends in these species are the loss of glands (present, however, in *firma*), thickened subcoriaceous texture with prominent raised veins, reduced lower pinnae few or none, and creeping rhizome.

The most aberrant element in sect. *Amauropelta* and one that I place here only hesitatingly is *Thelypteris minutula* Morton, from the páramo of Ecuador. The fronds are very narrow, densely glandular, and nearly exindusiate, with small, wiry stipes. Its closest ally may be *glutinosa* from Haiti.

Section *Amauropelta* has close affinities only to sections *Pachyrachis* and *Blennocaulon*.

24075 **5. Thelypteris sect. Blennocaulon A. Reid Smith, sect. nov.**

Rhizomata crassa, erecta; frondes volutae mucosae; aerophora praesentia, saepe prominentia; costae rhachidesque pilis septatis elongatis praeditae; segmenta basalia basiscopica pinnarum prolongata; laminae subtus glandulis sessilibus praeditae; venae saepe fuscatae, subtus subimmersae; sori submarginales, indusiati vel interdum exindusiati.

TYPE: *Aspidium cheilanthoides* Kunze [≡ *Thelypteris cheilanthoides* (Kunze) Proctor]. 7432

Perhaps 10 species, mostly at middle elevations, from southern Mexico, Jamaica, and Hispaniola to Bolivia, southeastern Brazil.

Nephrodium atomiferum Sod.*, *Dryopteris bañiensis* Rosenst.*, *Aspidium cheilanthoides* Kunze, *Dryopteris cheilanthoides* (Kunze) C. Chr. var. *eglandulosa* C. Chr. in Christ, *Thelypteris cheilanthoides* (Kunze) Proctor var. *mucosa* A. Reid Smith*, *Aspidium decrescens* Kunze ex Mett., *Dryopteris deflectens* C. Chr.*, *Dryopteris densa* Maxon*, *Lastrea grossa* Presl, *Aspidium kunzei* Fée [≡ *Dryopteris oochlamys* C. Chr.], *Dryopteris lanipes* C. Chr.*, *Dryopteris lanipes* f. *minor* C. Chr.*, *Dryopteris limaensis* Copel.*, *Dryopteris mertensioides* C. Chr., *Dryopteris multiformis* C. Chr.*, *Polypodium nitens* Desv., *Dryopteris opposita* (Vahl) Urban var. *mettenii* f. *major* Rosenst.*, *Dryopteris pabstii* Brade*, *Nephrodium resinoso-foetidum* Hook.*, *Nephrodium rigescens* Sod., *Polypodium ruizianum* Klotzsch*, *Nephrodium sprengelii* (Kaulf.) Hook var. *persicinum* Jenm., *Dryopteris supina* (Sod.) C. Chr. var. *biolleyi* Christ.

Section *Blennocaulon* is close to sect. *Pachyrachis* and also to certain species of sect. *Amauropelta* (*T. opposita*). From both of these, sect. *Blennocaulon* usually can be distinguished by the presence of pluricellular hairs on the veins and major axes, by the slightly immersed and blackened veins, and by the somewhat elongate basal basiscopic segments.

Certainly a few exindusiate species belong here, i.e., *deflectens*, *multiformis*, *nitens*, and *ruizianum*. These four are also somewhat atypical in having medial or inframedial sori. Within sect. *Blennocaulon*, I believe these characters (exindusiate, medial sori) are derived. A revision of the species is needed.

24074 **6. Thelypteris sect. Pachyrachis A. Reid Smith, sect. nov.**

Rhizomata erecta; frondes volutae mucosae; laminae deorsum gradatim angustatae (Typus III); aerophora praesentia, saepe prominentia; costae rhachidesque epilosae; costae subtus paleis appressis tenuibus stramineis vestitae; laminae subtus glandulis sessilibus rubris vel aurantiacis praeditae; sori mediales, indusiis magnis persistentibus glabris.

TYPE: *Aspidium pachyrachis* Kunze ex Mett. [≡ *Thelypteris pachyrachis* (Kunze ex Mett.) Ching]. 9441

About 10 species, at middle elevations, from the Greater Antilles (Jamaica, Hispaniola), southern Mexico (Oaxaca, Chiapas), Central America, Venezuela to Bolivia, and southeastern Brazil.

Aspidium berteroanum Fée, *Dryopteris consanguinea* (Fée) C. Chr. var. *aequalis* C. Chr.*, *Nephrodium crassipes* Sod., *Aspidium elatior* Fée*, *Dryopteris germaniana* (Fée) C. Chr. var. *glandulosa* C. Chr., *Aspidium helveolum* Fée*, *Dryopteris hieronymusii* C. Chr.*, *Dryopteris illicita* Christ, *Nephrodium jenmanii* Bak. ex Jenm.*, *Nephrodium jenmanii* Bak. ex Jenm. var. *sitiorum* Jenm., *Dryopteris malangae* C. Chr.*, *Thelypteris oaxacana* A. Reid Smith*, *Aspidium pachyrachis* Kunze ex Mett., *Dryopteris pachyrachis* (Kunze ex Mett.) Kuntze var. *bogotensis* C. Chr., *Nephrodium palustre* Bak. in Hook & Bak. [≡ *Thelypteris metteniana* Ching], *Aspidium platyrachis* Fée*, *Dryopteris riopardensis* Rosenst.*, *Nephrodium sprucei* Bak. in Hook. & Bak.*, *Aspidium tablanum* Christ*, *Aspidium tenerrimum* Fée*.

The relationship of sect. *Pachyrachis* is certainly with sect. *Blennocaulon* and sect. *Amauropelta*. The lamina and axes are without hairs, but sessile, reddish glands similar to those found in sect. *Amauropelta* occur on the leaf tissue below in most species. The stramineous to tan, adpressed costal scales are wholly unlike those found in species of sect *Lepidoneuron*. Indusia are generally larger and more easily seen than in any of the other sections of the subgenus.

24028

7. Thelypteris sect. Lepidoneuron A. Reid Smith, sect. nov.

Rhizomata plerumque erecta vel suberecta, raro repentia; pinnae inferiores abrupte reductae, remotae, glandiformes (Typus IV); costae subtus paleis brunneis, subclathratis et pilis appressis praeditae; laminae eglandulosae; sori indusiis destituti.

—2635

TYPE: *Polypodium rude* Kunze [≡ *Thelypteris rudis* (Kunze) Proctor].

Perhaps 50 species, from Mexico (2 species) and the Greater Antilles (ca. 3 species) to Bolivia, and southeastern Brazil (2 species), but primarily Andean, with the greatest number of species at middle to higher elevations in wet, mountainous areas of Colombia, Ecuador, and Peru.

Dryopteris abbottiana Maxon*, *Dryopteris alfredii* Rosenst.*, *Thelypteris antillana* Proctor*, *Dryopteris arborea* Brause, *Dryopteris atropurpurea* Hieron.*, *Dryopteris bonapartii* Rosenst., *Dryopteris boqueronensis* Hieron.*, *Dryopteris bradei* Christ*, *Dryopteris bradei* var. *palmensis* Rosenst., *Dryopteris brausei* Hieron.*, *Dryopteris caeca* Rosenst., *Dryopteris canelensis* Rosenst., *Nephrodium caucaense* Hieron.*, *Dryopteris cochaensis* C. Chr.*, *Nephrodium corazonense* Baker*, *Polypodium crossii* Baker*, *Phegopteris ctenoides* Fée, *Polypodium demeraranum* Baker*, *Dryopteris dumetorum* Maxon*, *Nephrodium elegantulum* Sod., *Dryopteris engelii* Hieron., *Polypodium euchlorum* Sod., *Dryopteris euchlora* (Sod.) C. Chr. var. *inaequans C. Chr.*, *Gymnogramme expansa* Fée, *Aspidium glaziovii* Christ, *Aspidium gleichenioides* Christ, *Dryopteris heineri* C. Chr.*, *Dryopteris herzogii* Rosenst.*, *Dryopteris horrens* Hieron., *Phegopteris impressa* Fée, *Dryopteris intromissa* C. Chr.*, *Dryopteris jimenezii* Maxon & C. Chr.*, *Phegopteris laevigata* Mett. ex Kuhn *[≡ *Polypodium lechleri* Bak.], *Nephrodium lasiopteris* Sod., *Nephrodium lustratum* Hieron.*, *Dryopteris macbridei* C. Chr. & Maxon*, *Dryopteris millei* C. Chr., *Thelypteris muscicola* Proctor*, *Dryopteris muzensis* Hieron.*, *Polypodium nervosum* Klotzsch*, *Gymnogramme patula* Fée, *Polypodium pavonianum* Klotzsch*, *Dryopteris pavoniana* (Klotzsch) C. Chr. var. *contracta* Hieron., *Dryopteris perstrigosa* Maxon*, *Dryopteris peruviana* Rosenst., *Dryopteris phacelothrix* C. Chr. & Rosenst.*, *Alsophila pilosa* Mart. & Gal., *Nephrodium piloso-hispidum* Hook., *Dryopteris pittieri* C. Chr.*, *Aspidium pterifolium* Mett. ex Kuhn, *Polypodium pteroideum* Klotzsch, *Dryopteris pteroidea* (Klotzsch) C. Chr. var. *subsagittata* C. Chr., *Nephrodium retrorsum* Sod., *Dryopteris roraimense* Brause, *Dryopteris rosenstockii* C. Chr.*, *Polypodium rude* Kunze, *Dryopteris rudis* (Kunze) C. Chr. var. *gradata* C. Chr., *Dryopteris rusbyi* C. Chr., *Dryopteris rusbyi* var. *major* Rosenst.*, *Nephrodium semilunatum* Sod., *Dryopteris silviensis* Hieron.*, *Dryopteris strigifera* Hieron.*, *Aspidium subdecussatum* Christ, *Nephrodium tetragonum* Presl, *Dryopteris utanagensis* Hieron.

Two Lesser Antillean species (*musicola, antillana)* are tentatively placed here, but they differ from most other members of sect. *Lepidoneuron* in having minute indusia.

Several evolutionary trends are discernible within sect. *Lepidoneuron*. The most noticeable is for the lamina to be more dissected (bipinnate-pinnatifid in *pteroidea* and *glaziovii*). Often correlated with this greater dissection is the tendency for the segments to be reflexed. Another trend is for loss of indument (hairs and/or scales). This can be seen in *caucaensis* and *laevigata*. Dark, sometimes polished stripes and rachises are yet another trend in several South American

species (*pavoniana, atropurpurea, laevigata, arborea).*

8. Thelypteris sect. Blepharitheca A. Reid Smith, sect. nov.

Rhizomata erecta; stipites rhachidesque fuscae, pilis densis brevissimis uniformibus infra 0.1 mm longis vestitae; pinnae inferiores sensim reductae (Typus III); costae, costulae, venae et plerumque laminae utrinque pilis similibus praeditae, eglandulosae; costae paleis destitutae; indusia nulla vel minutissima; sporangia setulosa vel glabra.

TYPE: *Polypodium concinnum* Willd. [≡ *Thelypteris concinna* (Willd.) Ching].

About 5 species, at middle elevations, on shady banks, in ditches, and along forest margins, from the Antilles, southern and eastern Mexico, Central America, Venezuela, Colombia to Bolivia and northwestern Argentina, and southeastern Brazil.

Dryopteris christensenii Christ, *Polypodium concinnum* Willd., *Phegopteris elongata* Fourn., *Phegopteris leptoptera* Fée, *Polypodium molliculum* Kunze ex Link, *Nephrodium stenophyllum* Sod.*, *Gymnogramme stierii* Rosenst.*.

The affinities of sect. *Blepharitheca* are uncertain. In some respects it approaches the *T. oligocarpa* group, especially *atrorubens* (sect. *Uncinella*). It is apparently not closely related to any of the other exindusiate sections.

9. Thelypteris sect. Apelta A. Reid Smith, sect. nov.

Rhizomata erecta; stipites rhachidesque stramineae, glabrae, stipites basi denigrati; aerophora nulla; laminae tenues, eglandulosae pinnarum inferiorum 2–4 paribus gradatim reductis, pinnis infimis auriculiformibus; costae subtus epaleatae, glabrae vel pilis dispersis patentibus praeditae; indusia nulla.

TYPE: *Nephrodium deflexum* Presl [≡ *Thelypteris deflexa* (Presl) Tryon].

In wet mountainous areas at middle to higher elevations, from Hispaniola, southern Mexico, Central America, Venezuela, and British Guiana to Peru.

Dryopteris assurgens Maxon*, *Nephrodium deflexum* Presl [≡ *Dryopteris lindigii* C. Chr.], *Polypodium roraimense* Baker*, *Dryopteris sellensis* C. Chr.*, *Aspidium simplicissimum* Christ.

A small section of uncertain affinities, in need of critical study to determine the number of species. Section *Apelta* is closest to and perhaps derived from sect. *Lepidoneuron* or sect. *Uncinella*. In texture (thin) and blade shape it is closer to the latter, but in lack of any trace of an indusium and in its near glabrousness, it approaches species such as *T. caucaensis* (sect. *Lepidoneuron*).

NAMES OF UNCERTAIN POSITION

Aspidium alfarii Christ [=*Aspidium strigosum* Christ, non Willd.], *Lastrea aristeguietae* Vareschi, *Nephrodium crenulaeum* Jenm., *Aspidium confluens* Fée, *Lastrea cumingiana* Presl, *Phegopteris delicatula* Fée, *Nephrodium cinereum* Sod., *Aspidium eriosorum* Fée, *Aspidium frigidum* Christ, *Polypodium involutum* Desv., *Dryopteris tablaziensis* Christ, *Nephrodium negligens* Jenm., *Thelypteris nubicola* de la Sota, *Aspidium producens* Fée, *Dryopteris rudiformis* C. Chr., *Polypodium ruffum* Poir., *Dryopteris sancta* (L.) Kuntze var. *ecuadorensis* Bosco, *Nephrodium stramineum* Sod., *Nephrodium supinum* Sod., *Dryopteris tamandarei* Rosenst., *Aspidium tenuiculum* Fée, *Aspidium van-heurckii* Fourn.

EXCLUDED NAMES

Below are names that I exclude from *Thelypteris* subg. *Amauropelta* but that have been included by Christensen and other authors under what I regard as synonyms of the subgenus.

Phegopteris blanda Fée [≡ *Thelypteris* (*Goniopteris*) *blanda* (Fée) Reed], *Phegopteris caespitosa* Fourn. [=*Thelypteris* (*Goniopteris*) *blanda*], *Dryopteris cabrerae* Weatherby [=*Thelypteris*

(*Thelypteris*) sp.], *Nephrodium etchichuryi* Hicken [=*Thelypteris* (*Goniopteris*) sp.], *Dryopteris guentheri* Rosenst. [=*Polybotrya*? certainly not *Thelypteris*], *Dryopteris mexiae* C. Chr. [=*Thelypteris* (*Steiropteris*) sp.], *Polypodium pubescens* Raddi [probably a *Ctenitis*], *Dryopteris tremula* Christ [=*Thelypteris* (*Thelypteris*) sp.], *Aspidium velatum* Kunze ex Mett. [=*Ctenitis* sp.].

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SHORTER NOTE

ADIANTUM CAPILLUS-VENERIS IN PENNSYLVANIA.—On May 12, 1974, I discovered a colony of *Adiantum capillus-veneris* L., the Southern Maidenhair, growing on the walls of a storm drain on Drexel Avenue in Lansdowne, Delaware County, Pennsylvania. This colony probably represents a temporary occurrence of this subtropical species which, according to Wherry's "Fern Guide," in the eastern United States is known sporadically as far north as southern Virginia and Kentucky. Specimens have been deposited in the herbarium of the Academy of Natural Sciences of Philadelphia (PH).—*Michael E. Kachur, Department of Botany, Academy of Natural Sciences, Nineteenth and the Parkway, Philadelphia, PA 19103.*

REVIEW

"INDEX FILICUM AND SUPPLEMENTS I–III," by Carl Christensen, ca. 1219 pp. 1905–1934, reprint 1973. Ca. $105.00.—Pteridologists are fortunate in having a world-wide index to the species of ferns. Carl Christensen published the first volume of his "Index Filicum" in Copenhagen during the years 1905–1906. It included the names of ferns published from 1753 to the end of 1905. At the beginning of the "Index" is a list of genera, subgenera, and sections, with synonymy, in a taxonomic arrangement as Christensen saw them. (A revised list appears at the beginning of the third supplement.) The "Index" attempted to assess the taxonomic validity of the species as Christensen understood them or accepted them from monographs prepared by other workers. The species that Christensen thought were synonyms are referred to the species he accepted, but the synonymies given under the accepted species are not always complete. Recently F. A. Stafleu (Taxon **22:** 465–466. 1973) commented on the taxonomic background of the "Index Filicum" and made some interesting observations on Christensen's life and work. Those few species that Christensen could not place are listed (in italics) as dubious. Some *nomina nuda* are also included. Considering that the "Index" was published early in Christensen's career, his judgements have proved to be remarkably sound (although, of course, today's generic concepts differ somewhat from those of 70 years ago).

Christensen published supplements in the same taxonomic style in 1913 (for 1906–1912), in 1917 (for 1913–1916), and in 1934 (for 1917–1933). The first two of these divided the names newly published from those that were corrections to entries in the previously published parts. In the third supplement, the entries to be corrected were combined with the new entries. Lists of addenda and corrigenda are printed on pages 660–670 of the original "Index" and on pages 196–200 of the third supplement. These should not be overlooked in searching for names in the "Index" and its supplements.

At least parts of the "Index" have been out of print for some time, and now Otto Koeltz Antiquariat, Postfach 129, 624 Königstein-Taunus, Federal Republic of Germany, has reprinted the original "Index Filicum" in one volume and Supplements I through III in another. The 1905–1906 volume (ISBN 3-87429-048-4) sells for DM 265, and the three supplements (ISBN 3-87429-049-2) for DM 170. The reprints are reduced in page height by about 7.5% from the original volumes, but this in no way interferes with the legibility or usability of these clearly printed and strongly bound books. The original indices were printed at a time when paper chemistry had not solved fully the problem of deterioration, and so hard users and libraries will be gratified that their reprint volumes will last longer than the original ones.—D. B. L.

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American Fern Journal

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Dr. John T. Mickel, New York Botanical Garden, Bronx Park, Bronx, New York 10458, is editor of the newsletter "Fiddlehead Forum." The editor welcomes contributions from members and non-members, including miscellaneous notes, offers to exchange or purchase materials, personalia, horticultural notes, and reviews of non-technical books on ferns. Foray and officer's reports, membership lists, and membership additions and changes of address are also published.

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Mr. Neill D. Hall, 1230 Northeast 88th Street, Seattle, Washington 98115, is Director. Spores exchanged and collection lists sent on request.

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Ferns of the Bahamas Including Caicos and Turks Islands

DONOVAN S. CORRELL*

The recent discovery of *Osmunda regalis* L. var. *spectabilis* (Willd.) A. Gray on Great Abaco *(Correll 42810)* represents another family of plants new to the Bahamian archipelago. This, along with the earlier discoveries of *Thelypteris ovata* R. St. John *(Correll & Godfrey 41486)* on North Andros (determined by Alan R. Smith) and *Schizaea poeppigiana* Sturm in a dense broadleaf coppice on Great Abaco *(John Popenoe & Jack Patterson 14)*, brings to six the number of fern species that have been added to the Bahama Islands flora since the 1920 publication of Britton and Millspaugh's "The Bahama Flora." Those species previously reported as new to the flora are *Pteris vittata* L. *(Gillis 7323* and *Popenoe 132)* from Great Abaco, *Thelypteris dentata* (Forssk.) E. St. John *(Correll 40856)* from Great Exuma, and *Trismeria trifoliata* (L.) Diels *(Gillis 7328A* and *Popenoe 131)* from Great Abaco. Undoubtedly, other fern additions can be expected from the Islands as exploration continues. To date, 36 species of true ferns and fern allies are considered to be in the flora of the Bahama Islands.

The *Osmunda* was found growing in fresh-water marshes and ponds covering several acres just below a north-south ridge in an open pineland (called a "pineyard" by local people) a short distance north of Marsh Harbour. I counted more than twenty clumps of plants. Some of the clumps had survived burning that had occurred when the ponds were desiccated during the dry season. In addition to the *Osmunda,* I have found *Acrostichum danaeifolium* Langsd. & Fisch., *Trismeria trifoliata,* and *Blechnum serrulatum* L. C. Rich. in wet habitats on various islands. Although it was included by Britton and Millspaugh as being in the flora, there is some question regarding the actual occurrence of *Acrostichum aureum* L. in the Bahamas.

Several "moisture-loving" species of limited occurrence have been found only on Inagua *(Marsilea nashii* Underw.), Acklin's and South Caicos *(M. vestita* Hook. & Grev.), and Abaco and Andros *(Selaginella armata* Baker). A continued search is being made to determine if these species occur in other areas of the Bahamas.

Distribution of some fern species in the Bahama Islands follows a distinctive ecological pattern, but others seem to have no definite pattern. With or without the occurrence of fires in the pineyards of *Pinus caribaea* Morelet that are found on Abaco, Andros, Grand Bahama, and New Providence, *Anemia adiantifolia* (L.) Swartz and *Pteridium aquilinum* var. *caudatum* (L.) Sadeb. are essentially uncritical in their habitat requirements. The latter species becomes an obnoxious weed in some areas by forming almost impenetrable masses. Only in marshy areas and in intervening dense broadleaf coppices are these species entirely lacking or greatly reduced in occurrence.

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Orchids and bromeliads grow in the coppices along with such species as *Polypodium polypodioides* (L.) Watt, *P. heterophyllum* L., *P. phyllitidis* L. and its var. *latum* (Moore) Proctor, *Paltonium lanceolatum* (L.) Presl, and *Psilotum nudum* (L.) Pal. Beauv. These occur on tree trunks, fallen logs, and on exposed rock ledges and walls.

The solution pits, sink-holes, "banana holes," or whatever one may call them, that are formed in the aeolian limestone that is the primary stratum for the Bahama Islands, whether in pineyards, broadleaf evergreen coppices, savannas, or dwarf coastal coppices, vary in width and depth from a few feet to as much as twenty feet or more. These more shaded and moist habitats often have one or more species of ferns on their walls or growing on their humus-covered floor. One such hole in a dense coppice on Great Exuma was so deep that it was possible to harvest the banana bunches at common ground level from the banana plants growing in its bottom. The walls of this hole and the jumble of fallen boulders on its bottom were covered only with a dense cloak of *Asplenium dentatum* L. Oddly enough, in another nearby hole no *Asplenium* was to be found, but the walls were covered with *Tectaria lobata* (Poir.) Morton, *Anemia adiantifolia* (L.) Swartz, and *Thelypteris reptans* (J. F. Gmel.) Morton. In a pit on North Andros in a mixed pine-hardwood forest only the other two species of *Anemia* known from the Bahamas were found—*A. cicutaria* Kunze and *A. wrightii* Baker. In other pits in the same general area only *Thelypteris cordata* (Fée) Proctor, *T. augescens* (Link) Munz & I. M. Johnst., and *T. normalis* (C. Chr.) Moxley were found. The latter two species, along with *T. dentata* (Forssk.) E. St. John, also occur on ledges, moist banks, and on the edge of coppices.

Species that occur in "banana holes," as well as in dense coppices generally, are *Adiantum tenerum* Swartz and *Sphenomeris clavata* (L.) Maxon. The latter is also found occasionally on open banks and among rocks, especially where moisture is available.

Also to be found rather frequently on banks, on the edges of coppices, in disturbed soils, or in savannas, especially in and about pineyards, is *Pteris longifolia* L. Found less frequently in rocky-grassy soils is *P. vittata*.

Two Bahamian species favor the leaf "boots" of old arborescent palmettos as their habitat. These are the rather widespread *Polypodium aureum* L. and the less common *Vittaria lineata* (L.) J. E. Smith.

Several species have been found at only one or two stations in the Bahamas. I have, as yet, not been able to extend the area of distribution in the Islands for any of these species. They are *Adiantum melanoleucum* Willd. from Eleuthera and New Providence, *Pityrogramma calomelanos* (L.) Link and *Polypodium squamatum* L. from Andros, *Tectaria heracleifolia* (Willd.) Underw. from New Providence, and *Nephrolepis biserrata* (Swartz) Schott from East Caicos. I have found, however, several localities for the ruderal *Nephrolepis exaltata* (L.) Schott.

I wish to acknowledge National Science Foundation support of my Bahama Flora research (Grant No. GB-41190X), and the assistance and cooperation of various individuals during the course of my exploratory work in the Bahamas.

Geographic Patterns in Temperate American Ferns and Some Relationships in Thelypteris

ALICE TRYON and ROLLA TRYON*,[1]

Detailed studies of species along with analyses of floristic ensembles have resulted in a better understanding of the history of the flora of the United States and Canada. This study of the chromosomes, spores, and geographic relationships of *Thelypteris nevadensis* (D.C. Eaton) Morton illustrates how such diverse data can be synthesized and are applicable to broader phytogeographic concepts. This fern of moist, open meadows and wooded slopes ranges from southern British Columbia to central California and geographically is a critical species. Its closest relative is *T. noveboracensis* (L.) Nieuwl. of eastern North America; also it is related to other species of eastern Asia. Geographic analyses of these American species and other taxa having similar Cordilleran–Appalachian ranges show predominantly circumboreal affinities. There is a lesser element among the North American mesic ferns that has geographic relations with tropical regions. The cytological and palynological data illustrated here document basic information useful in establishing evolutionary lines and supplement other evidence pertaining to the geography and migration of species. This study has developed out of previous work on the alliance of three species of *Thelypteris* in north-eastern America (Tryon & Tryon, 1973).

CYTOLOGY

Thelypteris nevadensis has been reported to have chromosome numbers of $n=26$ and $n=27$ (Taylor & Lang, 1963), based on material from Vancouver Island, British Columbia. In that work the variability of the species is noted as, "sometimes giving counts of 26 and sometimes 27, which is a matter that should be investigated further." A gametic number for the species has been reported as 27 by A. R. Smith (1971) from collections made in Fresno County, California. In this publication, Smith regards the earlier report of $n=26$ as unlikely, although he cites "T. nevadensis ($n=26$ or 27)." Photographic records of these earlier reports have not been published. We have studied the meiotic chromosomes in material from the Cascades of Oregon, which clearly has 27 pairs (*Fig. 1*).

In *Thelypteris* there are reports establishing several chromosome numbers, among which $n=36$ is the most frequent and seems to be the basic number for the genus. In *Thelypteris palustris* Schott there are documented records of $n=35$ over the range of the species in eastern North America, Europe and Japan. A series of numbers, ranging from $n=29$ to $n=32$, is also reported for other species of *Thelypteris*. These numbers suggest that chromosome deletion may have had an important role in evolution within the genus. There is a need for further cytological work in certain critical species to establish evidence for this. *Thelypteris*

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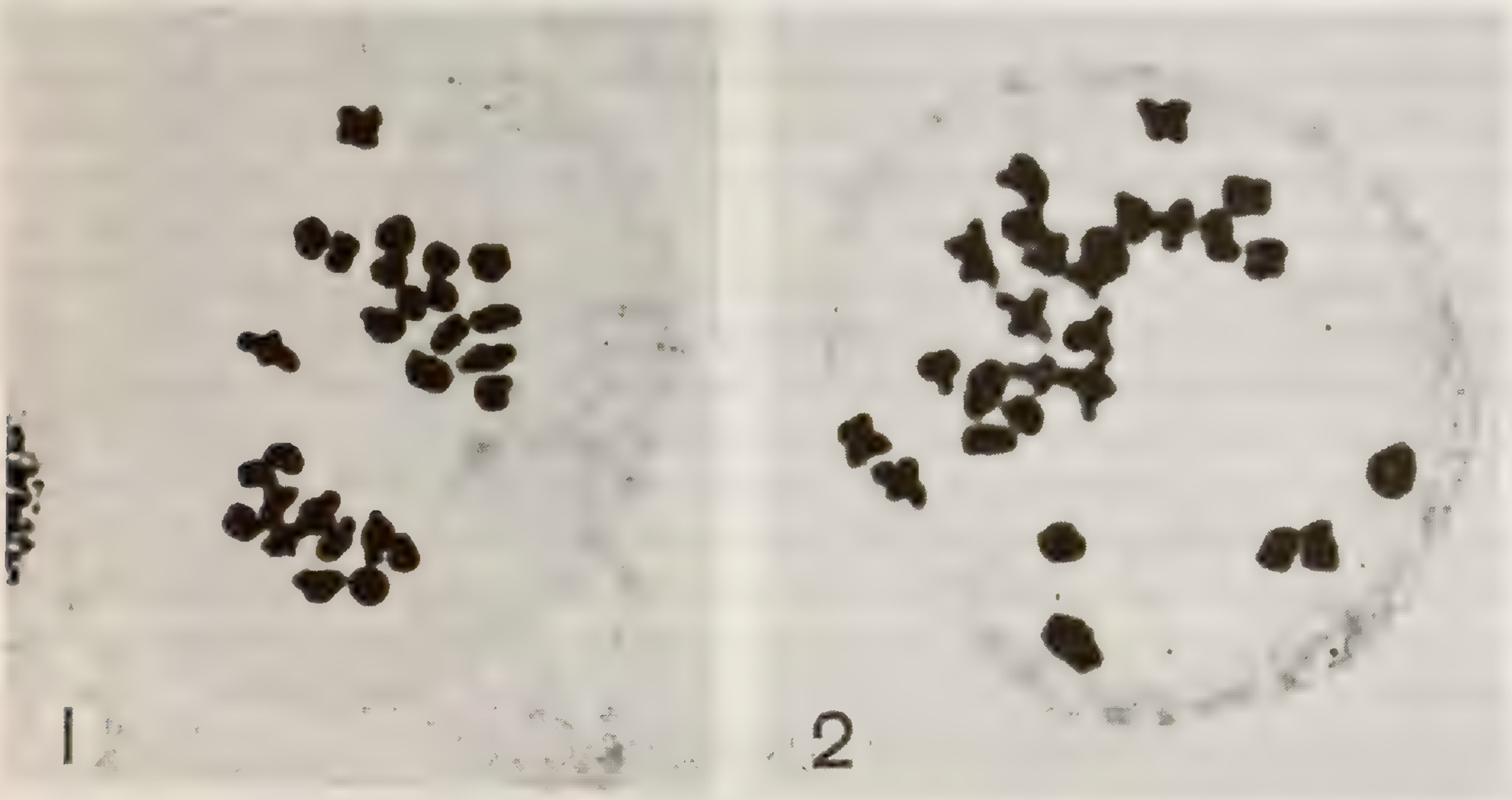
[1]We are grateful to Neill D. Hall for the material of *Thelypteris nevadensis* from the Cascades of Oregon, illustrated here. We are also appreciative for plants from British Columbia sent by Dr. T. M. C. Taylor. We are grateful to the Jeol Company, Medford, Mass. for use of the JSM-35 instrument and especially for the work of Aki Kabaya.

nevadensis may be one of the species in which cytological analyses of populations will yield data on aneuploidy. The earlier report of $n=26$ may be an accurate rather than an erroneous one due to difficult material. Additional work on the populations of Vancouver Island should easily resolve this matter. The report of $n=36$ in *T. palustris* from Japan has been altered to $n=35$ (Tryon & Tryon, 1973), but further study should be made of populations of that species throughout its range in Asia, as well as in Africa and New Zealand.



Meiotic chromosomes of *Thelypteris* with 27 bivalents, × 1300. FIG. 1. *T. nevadensis, N. D. Hall* in 1973, east of Salem, Cascade Mts., Oregon (GH). FIG. 2. *T. noveboracensis, A. Tryon 69-5*, Lincoln, Mass. (GH).

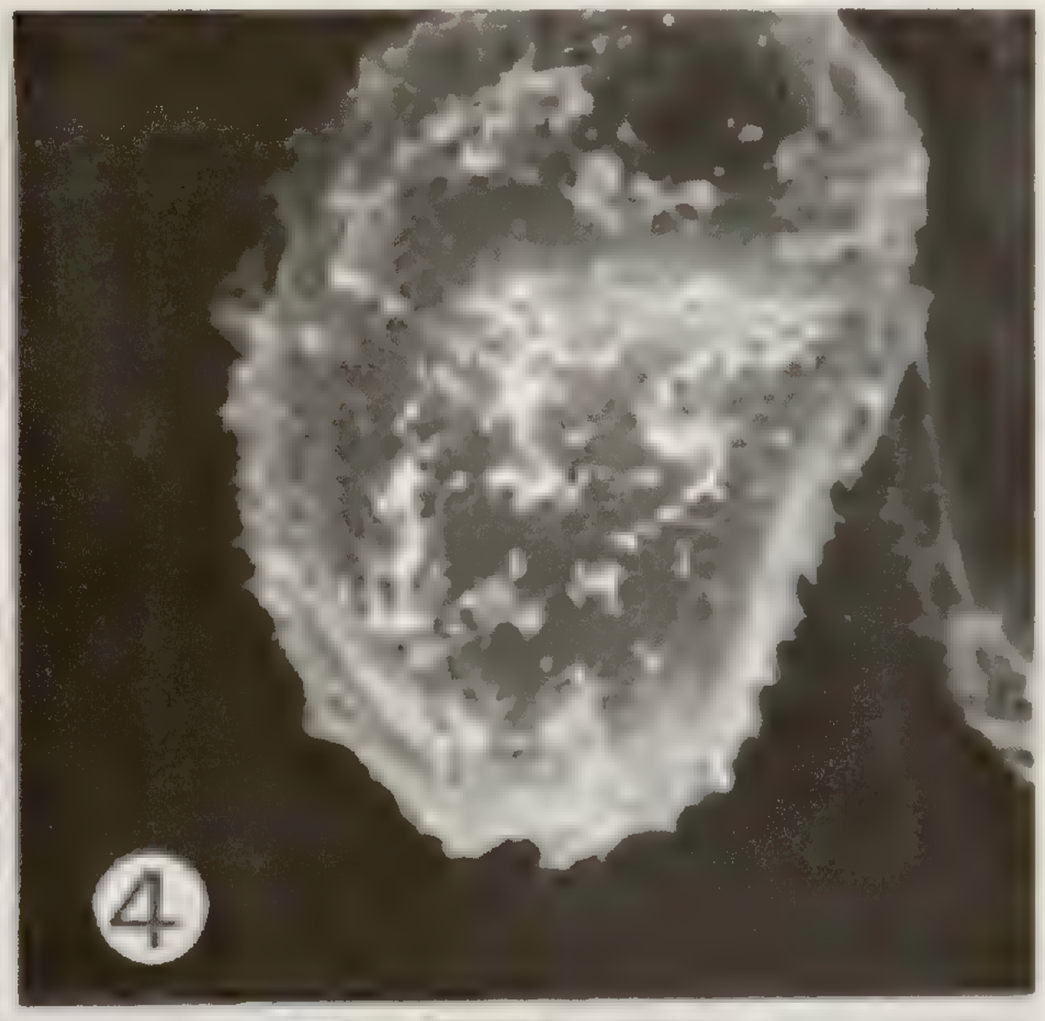
The report of $n=27$ in *Thelypteris noveboracensis*, as shown in *Fig. 2*, is consistent with other records for the species over its range in North America. Previous reports are summarized in our earlier work, cited above. The occurrence of the gametic chromosome number 27 is unique among American species of *Thelypteris*. It is known in only one other species, *T. cystopteroides* (D. C. Eaton) Ching (S. Kawakami, pers. comm. 1973), a rare species of Japan and the Ryukyu Islands. Although *T. nevadensis* and *T. noveboracensis* are clearly related, this third species is quite distinct. As the specific epithet implies, it is a smaller plant with the leaf architecture of *Cystopteris fragilis*. The leaves are almost glabrous, about 10 cm long, and the rhizomes are very slender and long-creeping. A detailed description of the species is given by Iwatsuki (1965, pp. 169–170). A basic question in *Thelypteris* cytology is whether the low number 27 is primitive and monophyletic or whether it is derived and possibly polyphyletic. The solution evidently lies among related species of eastern Asia, especially those recently placed in *Parathelypteris* by Holttum (1971). This group includes, among others: *Thelypteris glanduligera* (Kunze) Ching, with $n=72$, and *T. nipponica* (Franch. & Sav.) Ching and *T. japonica* (Baker) Ching, with $n=62$. *Thelypteris beddomei* (Bak.) Ching and *T. japonica* var. *musashiensis* Hiyama are reported with $n=31$, and *T. cystopteroides* has $n=27$.

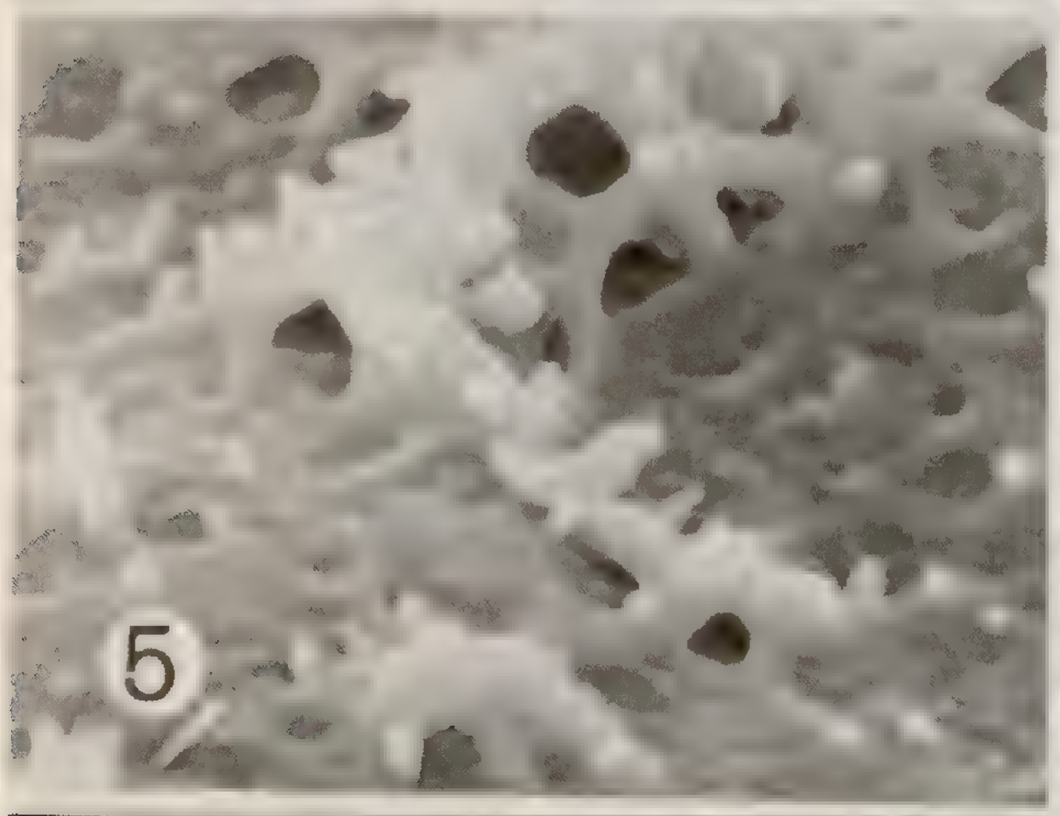
SPORES

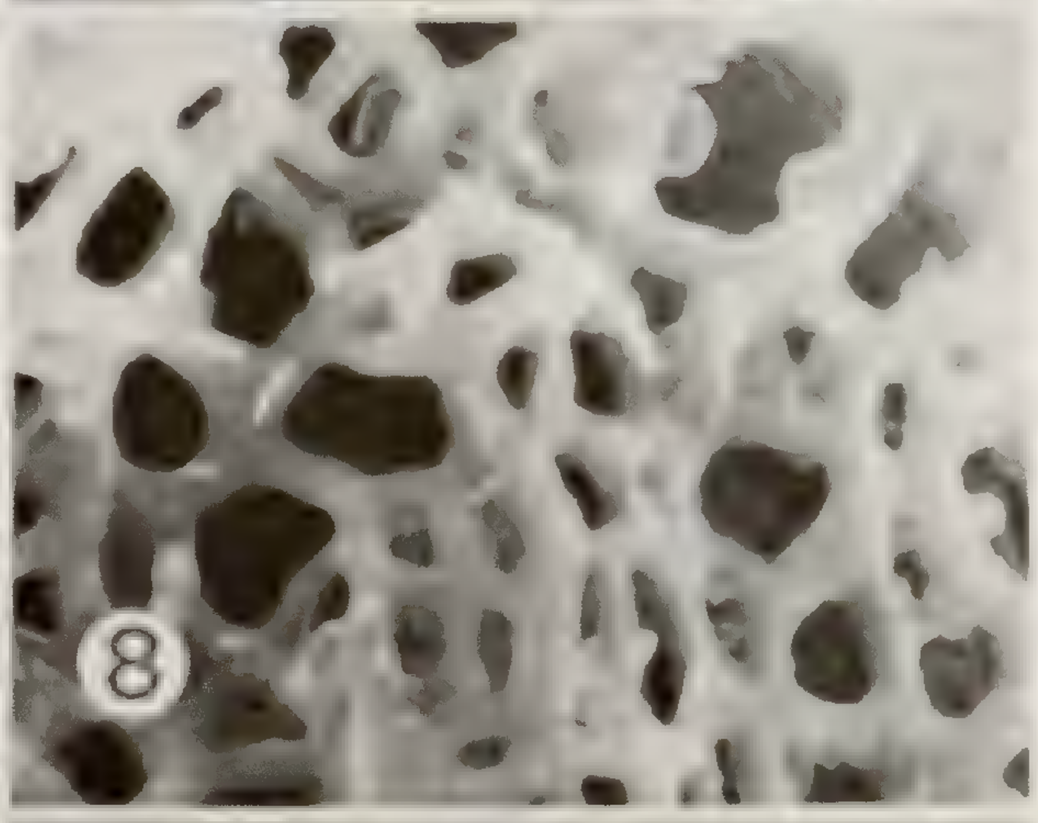
A new era in palynology has been initiated by the recent electron microscope studies of spores. Information revealed in scanning electron microscope photographs makes detailed descriptions superfluous and, indeed, emphasizes the lack of appropriate terminology. The study of spores of thirty species with the transmission electron microscope by B. Lugardon (1972) illustrates the complexity and variation in wall stratification. The SEM survey of the spores of Thelypteridaceae by C. Wood (1973), as well as our earlier work noted below, shows that surface patterns of spores have utility in systematic work.

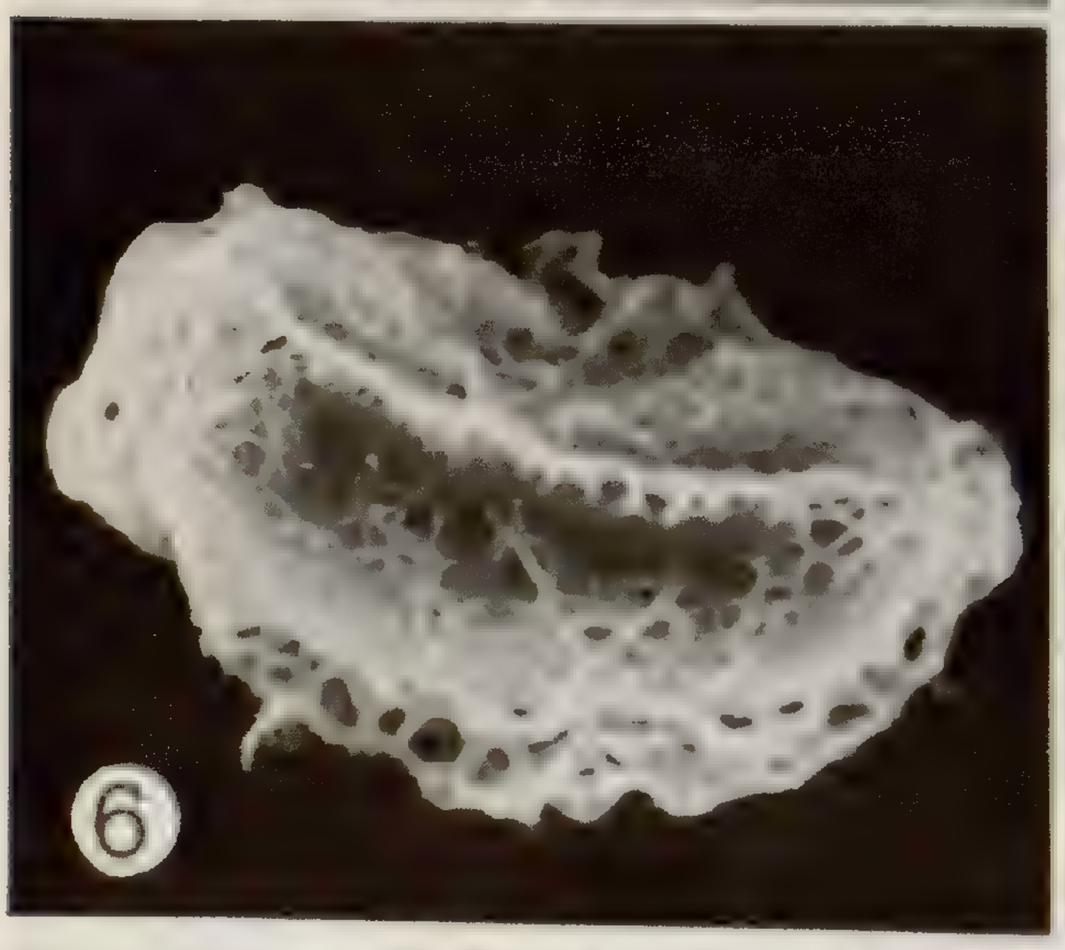
The spores examined here are from herbarium specimens. They were prepared as indicated by methods described in detail earlier (A. F. Tryon, 1971), consisting of underlaying with carbon prior to coating with an alloy of palladium–gold. The work was done with an AMR-900 instrument at the Gordon McKay Laboratories of Applied Science, Harvard University, and also with a JSM-35 instrument (designated by J in the figure legends). The basic similarities in surface structure of the spores of *Thelypteris nevadensis* and *T. noveboracensis* are evident in *Figs. 3–8*. The reticulum is less regular in the spores of *T. nevadensis* (*Fig. 5*), with ridges both appressed and projecting from the surface. In *Fig. 3* the commissural ridge extends more than half the length of the spore. *Thelypteris noveboracensis* spores in *Figs. 6–8* have a more prominent and uniform reticulum. The surface texture of some of the ridges as well as the underlying strata is apparent at the right of *Fig. 8*. The pattern of strongly reticulate ridges in these spores is similar to that of *T. nipponica* (Tryon & Tryon, 1973).

Wood's (1973) classification of Thelypteridaceae spores contains two basic groups: Type 1—Winged or Ridged, and Type 2—Reticulate. Each of these groups is subdivided into several classes. In this system the spores of *Thelypteris nevadensis* were included in the Reticulate group in the subdivision Reticulum spiny, which is described as, "Simple spines with ridged bases running together to form a reticulum adpressed to the underlying sporodermal surface." Spores of *T. nipponica* were placed in the first group among those with Winged sporoderm and in the subdivision described as, "Wings narrow, may be nearly membranous, usually with crenate or fimbriate crests. The wings may be tall or short and anastomosis of wings is common." The spores of *T. noveboracensis* were not included in this survey, but evidently they belong in the Reticulate group along with those of *T. nevadensis*. The great variety of surface structure among these thelypteroid spores includes such diverse forms described as winged, spiny, reticulate, and verrucate. These different types represent some of the subdivisions within the two major groups recognized by Wood. The information from these SEM studies raises more complex problems on the physiological development and evolutionary relations of the different forms. It appears that the diversity in spore structure may be a function of developmental physiology, rather than adaptation for dispersal. Marked differences also occur within species, as shown by variations of the sporoderm structure in *T. palustris* (A. F. Tryon, 1971) and in "*Dryopteris campyloptera*," noted by Britton (1972). Also compare the spores of *T. noveboracensis* in *Figs. 6* and *7* illustrated here.









Thelypteris spores. FIGS. 3–5. *T. nevadensis*, *N. D. Hall* in 1973, east of Salem, Cascade Mts., Oregon (GH). Reticulate perispore. FIG. 3. The commissural ridge diagonal and eroded perispore at lower right, ca. × 1300. FIG. 4. Spore with strongly appressed reticulum, ca. × 1300. FIG. 5. Perispore detail, ca. × 6000. FIGS. 6–8. *T. noveboracensis*, *A. Tryon 69-5*, Lincoln, Mass. (GH). Reticulate perispore. FIG. 6. The commissural ridge slightly above center, ca. × 1300. FIG. 7. Spore with strongly projecting reticulum, ca. × 1300. (J). FIG. 8. Perispore detail, irregular surface within areolae, top right, ca. × 5000.

GEOGRAPHY

Thelypteris nevadensis, ranging from southern British Columbia to central California, and *T. noveboracensis*, ranging from Newfoundland west to Wisconsin and south to Georgia and Louisiana, represent the well known Cordilleran–Appalachian floristic affinity among North American plants. Another similar vicarious species pair in ferns is *Dryopteris arguta* (Kaulf.) Watt (western) and *D. marginalis* (L.) A. Gray (eastern). These disjunct relations are also evident in the geographic distribution of varieties, as in *Polystichum braunii* (Spenner) Fée var. *alaskense* (Maxon) Hult. (western) and var. *purshii* Fern. (eastern). They also occur in single taxa which may be disjunct, as in *Athyrium distentifolium* Tausch [*A. alpestre* (Hoppe) Moore] and *Dryopteris cristata* (L.) A. Gray, or in those which have more or less continuous ranges, especially across the north, as in *Cystopteris montana* (Lam.) Bernh. and *Thelypteris phegopteris* (L.) Slosson.

Analysis of the floristic ensembles of ferns of the United States and Canada reveals some basic geographic information. Nearly all species with Cordilleran–Appalachian relations have broader circumboreal geographic affinities involving the same species or species groups also occurring in eastern Asia and/or in Europe. The dominant element among the mesic ferns of the United States and Canada has circumboreal relations. The mesic tropical species have not contributed significantly to our temperate or boreal fern flora, although there is a very rich reservoir of species immediately to the south. The principal tropical ferns in the United States are the West Indian element, strongly represented in Florida, and the Mexican xeric element, centering in the southwest from Texas to southern California. The basis for this dominance of circumboreal ferns in our flora is undoubtedly related to the series of continental glaciations and intervening mild interglacial periods during the Pleistocene. The poor representation of species of the wet tropics is quite possibly due to their requirement for gradual adaptations to more northern climates, which would not be met by the oscillating extremes during continental glaciation.

The boreal elements of the fern flora of North America, on the other hand, have been intimately involved with Pleistocene history. In contrast to a tropical fern flora, an originally more northern one, for example, in eastern Asia, would be well adapted to migration during interglacial periods, and some species would have the capacity for cold adaptation. Migration of species from eastern Asia could result in broad distributions in North America during an interglacial period. During the glacial maximum the ranges would be restricted south of the ice and especially to the east and west of the northern great plains. During the following interglacial, migration northward of some of the species would re-establish continuous ranges. Those species less cold-adapted would migrate little if at all and would remain geographically isolated. Divergence among these isolated populations could account for the differences in vicarious species pairs such as *T. nevadensis* and *T. noveboracensis*. The similarities that have been shown here between these species in chromosome number and surface structure of the spores indicate a relatively close relationship. This also suggests that their present Cordilleran and Appalachian floristic patterns may represent a relatively late geographic disjunction.

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Boughton Cobb (1894–1974)

Boughton Cobb was born in Lake Forest, Illinois, on June 18, 1894. His early years were spent in a rural community, where his love for the world of nature began. His family moved to Washington, DC when Boughton was still young. He liked to hunt and fish, but gradually his enthusiasm for observing nature pushed those earlier interests aside. He graduated from Harvard in 1915 and then trained as an architect at the Columbia School of Architecture. After serving in World War I, he engaged in a successful business career in textiles, from which he retired in 1960. The Cobbs had a summer home—later their permanent residence—in Falls Village, Connecticut, where Boughton was widely known and active in community affairs. The Cobb's attractive house had a terrace overlooking a fern-bordered brook. Boughton maintained a large collection of hardy American ferns and had a greenhouse for experimenting with unusual ferns. In the preparation of his book "A Field Guide to the Ferns," which was illustrated by his neighbor Laura Louise (Mrs. H. Lincoln) Foster, he spent two months ferning in the British Isles and visited several sections of this country. He participated in several forays and meetings of the American Fern Society, of which he was a life member. He died January 13, 1974, in New York City, leaving Mrs. Cobb (the former Edith McKeever), a son, a daughter, and seven grandchildren.—*Benjamin R. Allison, Hewlett, Long Island, NY 11557.*

A New Form of Asplenium montanum from New York

TIMOTHY REEVES*

On the Shawangunk Mountain ridge in Ulster County, New York, on September 18, 1973, I discovered 60 fronds of an unusual *Asplenium* growing in a fissure on a vertical cliff of Silurian conglomerate.

Asplenium montanum Willd. is abundant on these cliffs. I have observed numerous living plants of *Asplenium montanum* in Ulster County, New York, in seven counties in North Carolina, and I have seen herbarium specimens at the New York Botanical Garden (NY). All specimens were found to be uniform in morphology, and more than 99 per cent of the fronds bore sori. There are no described forms or varieties of this species.

The new form (*Fig. 1*) differs from the typical form in the following characters: (1) blades light yellow-green instead of dark blue-green, (2) tip of frond not tapered to a lobed apex (*Fig. 2A* versus *3A*), (3) pinnae and ultimate divisions more dissected (*Fig. 2B* versus *3B*), (4) frond length averages 2.3 cm shorter than typical New York specimens, and (5) the absence of sori. The possibility of ecological variation is minimal, as plants of the typical species grow on the same cliffs and even on both sides of the new taxon in the same rock fissure. These differences warrant naming this a new form of *Asplenium montanum*.

Asplenium montanum f. shawangunkense Reeves, f. nov.

Ab *Asplenio montano* f. *montano* lamina flavo-virenti sterili, apice non lobato, et pinnis lobisque incisioribus differt.

HOLOTYPE: Between Lake Minnewaska and Mohonk Lake in the Shawangunk Mountains, Ulster County, New York; in fissure on vertical cliff in deciduous woods; ca. 1170 ft, 18 Oct 1973, *Reeves 500* (ASU; isotypes MICH, NY).

The possibility that *A. montanum* f. *shawangunkense* might be a different species or of hybrid origin was investigated using paper chromatography, following the methods of Smith and Levin (Amer. J. Bot. **50**: 952–958. 1963). To compare my results with theirs, I prepared chromatograms from dried herbarium specimens of *Asplenium rhizophyllum* L., *A. platyneuron* (L.) Oakes, and *A. bradleyi* D. C. Eaton, as well as of *A. montanum*. All chromatograms I obtained were similar to those reported by Smith and Levin. The chromatograms of *A. montanum* from one New York and two North Carolina localities were indistinguishable from those of the new form. This strongly suggests that this form is not another species or of interspecific hybrid origin.

Apparently there are parallel situations occurring in other species (W. H. Wagner, Jr., pers. comm.): *Asplenium platyneuron* (L.) Oakes ex D. C. Eaton f. *hortonae* (Davenp.) L. B. Smith, *Polypodium vulgare* L. f. *cambricum* (L.) Broun, and *P. virginianum* L. f. *cambricoides* F. W. Gray, which are sterile and more finely dissected than their respective typical forms.

I wish to thank Daniel Smiley, Director of the Mohonk Trust, for permission to collect plants. Use of the New York Botanical Garden Herbarium (NY) and Library is gratefully acknowledged. Wendy Hodgeson prepared the illustrations.

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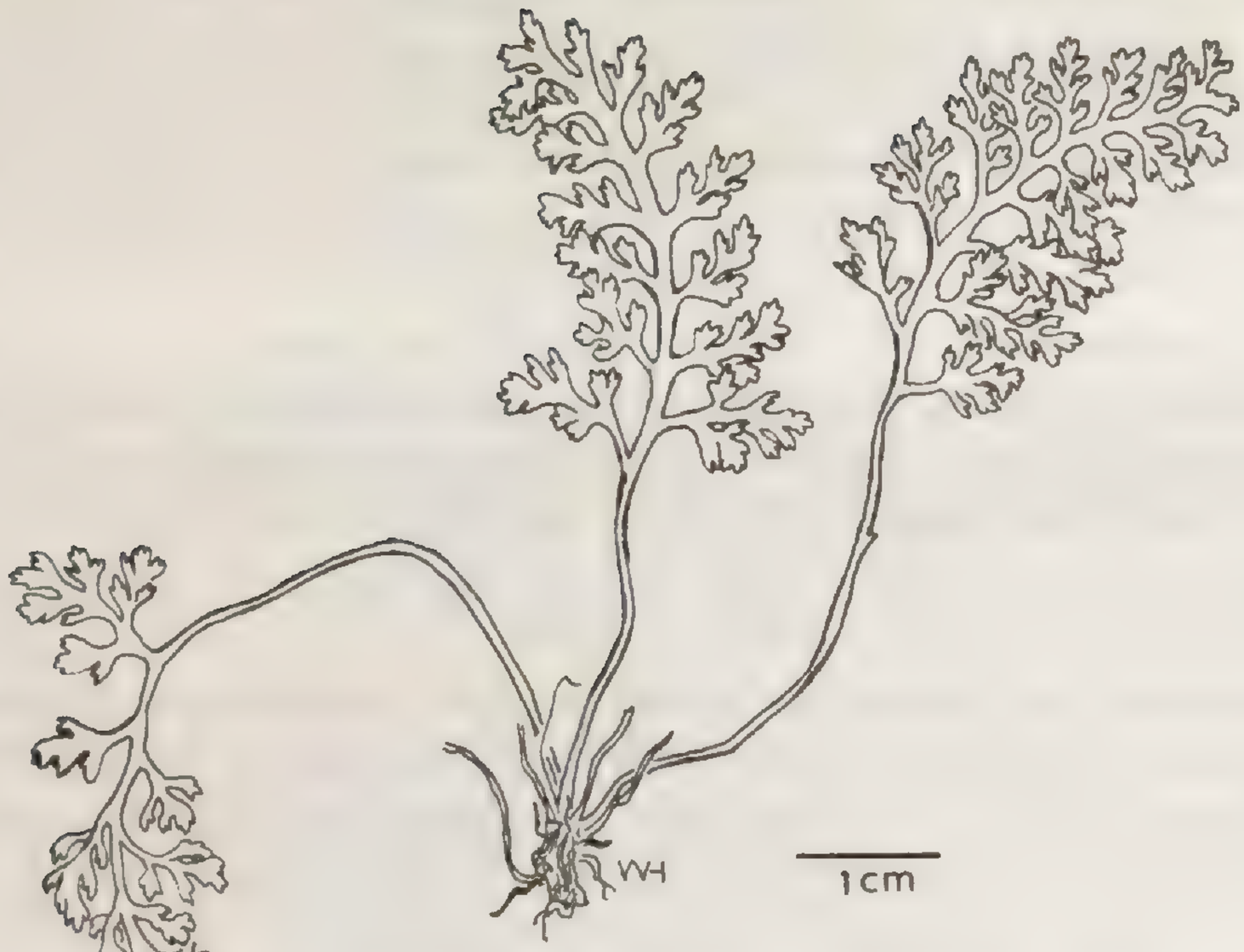
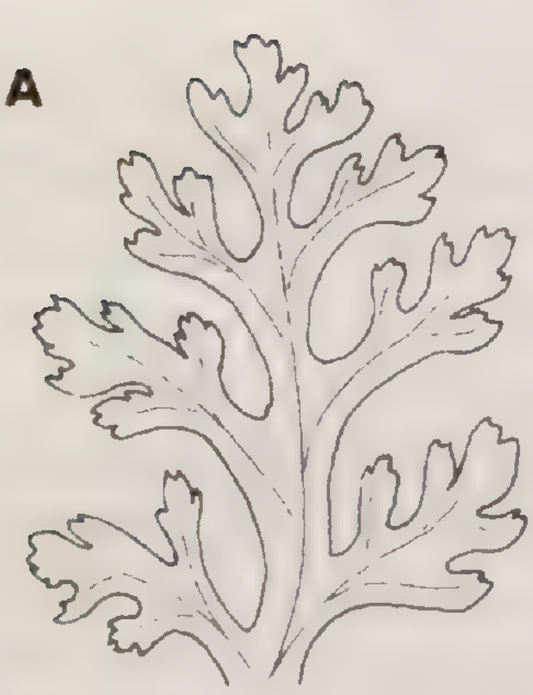
1



2A



2B

5 mm

3A

3B

FIGS. 1, 2. *Asplenium montanum* f. *shawangunkense*. FIG. 1. Holotype specimen. FIG. 2A. Frond apex. FIG. 2B. Basal pinna. FIG. 3. *Asplenium montanum* f. *montanum*. FIG. 3A. Frond apex. FIG. 3B. Basal pinna.

Notes on the Distribution of the Pteridophytes of Suriname

K. U. KRAMER*

In a forthcoming publication (Kramer, in prep.) floristic and taxonomic data of the pteridophyte flora of Suriname will be assembled, with keys and notes on their local distribution and ecological preference. The present paper deals with the geographical distribution of Suriname pteridophytes beyond the boundaries of Suriname (*Fig. 2*), a subject that lies beyond the scope of a local fern Flora.

In the past, some (but relatively not very many) authors of fern Floras included a paragraph on the distribution of the taxa (Posthumus, 1928; Christensen, 1932; Backer & Posthumus, 1939). In some other fern Floras some space is devoted to ecology, but very little to geography (Holttum, 1954). In still others, considerations of a general kind on ecology and geography are altogether lacking (Vareschi, 1969). Lyell (1870), in his rather little-known book on the distribution of ferns, tried to bring together all the data known at his time; his work is now, of course, almost exclusively of historical significance.

As far as pteridophytes are concerned, there is in Suriname virtually but a single environment—the forest—and as a whole our data on fern distribution are too scanty to differentiate between the various types of forest, as was done, for example, by Brownlie (1973) for the species of *Lindsaea* in Fiji. It is my impression, however, that in the future a number of fern species will prove to be indicators of certain forest types in Suriname, too. Ferns occurring exclusively on savannas are very few in number (mainly a few species of *Schizaea*). The same is true for ferns confined to rocks, like *Doryopteris conformis* Kramer & Tryon and *Pterozonium paraphysatum* (A. C. Smith) Lellinger; most epilithic species also grow frequently on tree bases or forest soil. The ferns preferring swamps and open water are equally few in number and are as a rule widespread.

The principal ecological categories which can be distinguished in the Suriname pteridophytes are epiphytes and terrestrial species. On rocks and shaded, mossy tree bases the two groups may meet, but by and large they are fairly sharply delimited. Therefore, I differentiate between epiphytes and terrestrial species by considering as epiphytes only pteridophytes that are completely or nearly confined to an epiphytic habitat. This excludes, among others, a number of *Asplenium* species often regarded as epiphytes, but which, in my experience, quite often are found on rocks, decaying wood on the forest floor, etc. Compare Morton and Lellinger (1966), where epiphytism in *Asplenium* is actually used as a key character, to which various objections may be raised.

There are, of course, pteridophytes that occur only in the "sub-cloud forests," which are montane forests that approach cloud forests on the loftiest chains and peaks in the center of Suriname. But in many cases it is very difficult to ascertain whether the species truly are confined to montane forests or have only been collected there more often. For instance, recently I found *Cyathea macrocarpa* (Presl) Domin and *Lindsaea parkeri* (Hooker) Kuhn near Zanderij in the lowland

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FIG. 1. Map of Suriname. FIG. 2. Map of northern South America and adjacent regions.

on the edge of the coastal plain (*Fig. 1*). These species otherwise are regarded as typical of the hills and mountains, or at least typical of the interior. The most likely category of species truly confined to the interior are those found on Roraima sandstone substrate and soils derived from it and which occur only in a limited area in the center of Suriname, e.g., *Pterozonium paraphysatum* (A. C. Smith) Lellinger, *Lindsaea pendula* Klotzsch, and *L. stricta* (Swartz) Dryand. var. *jamesoniiformis* Kramer. But even some of these may turn up in lowland savanna areas, as exemplified by *Lycopodium duidae* A. C. Smith var. *guianense* Kramer, one of the characteristic species of the Kappel Savanna on Roraima substrate at the foot of Tafelberg (Kramer & van Donselaar, 1968), but again known from one find near Zanderij. I think that only in the case of epiphytes of the "sub-cloud forest" may we be reasonably sure that they do not occur outside this vegetation type.

Very little can be said about geographical limits of species within the country, other than those of altitude and other ecological factors. For example, species found only in the west or south are as a rule known by so few collections that it would be highly speculative to draw conclusions from their presently known stations.[1] We probably may make an exception for the southern savannas, which straddle the Tumuc-Humac Mountains on the southern border of Suriname. A considerable number of angiosperms have their only (usually northernmost or easternmost) station in Suriname in this area, and the same may be true for some of the pteridophytes known in the country from this area alone: *Anemia ferruginea* H. B. K. var. *ahenobarba* (Christ) Mickel, *A. pastinacaria* Moritz ex Prantl, and *Doryopteris collina* (Raddi) J. Smith.

For conclusions of a general nature, we should thus focus our attention on the complete distribution of the species. I have tried to divide them into a number of groups representing certain distribution types, as was done by van Donselaar for savanna plants (1965, p. 75ff). I realize that this is not without risk in ferns, as their taxonomy in many cases is insufficiently understood and their areas often are not reliably known. Nevertheless, the figures may give some general impression of the phytogeographic ties of the fern flora of Suriname. For recent studies of a similar kind of fern floras of other areas, see Holttum (1964), Brownlie (1965), and Iwatsuki (1972, 1973). The number of comparable papers is, as far as known to me, quite small.

The figures may soon become outdated as further exploration adds more species to the list and as further study shows taxa here accepted as species to be aggregates. Posthumus's geographical account in his fern Flora of the Guianas (1928, pp. 173-185) is now almost entirely outdated.

What the figures do not tell us is how common the species are in Suriname, i.e., what part they play in the actual composition of the plant cover. According to my own impressions in the field, the fern flora of the rain forest floor is very strongly dominated by a small number of species: *Adiantum latifolium* Lam., *A. obliquum* Willd., *A. cajennense* Willd. ex Klotzsch, *A. terminatum* Kunze ex Miquel,

[1] *Schizaea incurvata* Schkuhr, common on savannas in the north, so far has not been found in eastern Suriname nor in French Guiana.

Lindsaea lancea (L.) Bedd., *L. guianensis* (Aubl.) Dryand., *L. dubia* Spreng., *Trichomanes pinnatum* Hedw., *T. cristatum* Kaulf. ex Poir., *T. vittaria* DC. ex Poir., and *Ctenitis protensa* (Afz.) Ching. Most other species are very much rarer. For the casual botanical observer, Suriname gives the impression of being the land of *Adiantum* and *Lindsaea*. The dominating epiphytes cannot be enumerated so readily, as it is difficult to obtain a true and complete picture of these rather inaccessible plants. In the lowland apparently several species of *Polypodium* subgenus (or genus) *Microgramma* predominate: *P. ciliatum* Willd., *P. lycopodioides* L., *P. persicariifolium* Schrad., as well as *P. aureum* L., *P. percussum* Cav., *P. crassifolium* L., and *P. phyllitidis* L. Other common epiphytes of this area are *Trichomanes pedicellatum* Desv., *T. ankersii* Parker ex Hook. & Grev. (these two perhaps more correctly called scandent hemiepiphytes), *Vittaria lineata* (L.) J. E. Smith, *Dicranoglossum desvauxii* (Klotzsch) Proctor, *Asplenium serratum* L., *Antrophyum guayanense* Hieron., and *Hymenophyllum polyanthos* (Swartz) Swartz. In the hills and mountains other species join or replace them, like *Xiphopteris serrulata* (Swartz) Kaulf., *Hecistopteris pumila* (Spreng.) J. Smith, and *Hymenophyllum hirsutum* Swartz.

Another point is the unexpected, apparent great rarity or even complete absence of some tropical American ferns which are otherwise widespread and often common elsewhere. Examples of locally rare, generally widespread species are: *Adiantum macrophyllum* Swartz, *Anemia phyllitidis* (L.) Swartz, *Blechnum occidentale* L., *Cyclopeltis semicordata* (Swartz) J. Smith, *Dennstaedtia obtusifolia* (Willd.) Moore, *Doryopteris pedata* (L.) Fée, *Hemidictyum marginatum* (L.) Presl, *Hypolepis repens* (L.) Presl, *Trichomanes polypodioides* L., and *T. hymenophylloides* v.d. Bosch. Most of these are known from only a single collection or a single locality.

Ferns that might be expected in Suriname because of their overall distribution but that have never been found so far include *Gleichenia bifida* (Willd.) Spreng., *Peltapteris peltata* (Swartz) Morton, *Polybotrya osmundacea* Humb. & Bonpl. ex Willd., *Polypodium fraxinifolium* Jacq., *P. lanceolatum* L., and *Pteris denticulata* Swartz.

DISTRIBUTION TYPES

The distribution of 286 species of pteridophytes occurring (or strongly suspected to occur) in Suriname seems to be at present sufficiently known. These may be divided into distribution types as follows. I have consciously avoided the term "flora element," as it is too much subject to ambiguous interpretation. For a discussion, see van Balgooy (1971, pp. 58–59). The distributions of the pteridophytes of Suriname discussed below are summarized in *Table 1*.

1. Pantropic Species.—These often extend far into subtropical areas, particularly in the south. This category includes 13 species (4.5% of the fern flora). Examples are: *Acrostichum aureum* L., *Ceratopteris thalictroides* (L.) Brongn., *Didymochlaena truncatula* (Swartz) J. Smith, *Psilotum nudum* (L.) Pal. Beauv., and *Thelypteris interrupta* (Willd.) K. Iwats. [=*T. totta* (Thunb.) Schelpe =*T. gongylodes* (Schkuhr) St. John in Small]. Some examples are probably taxonomic

aggregates, like *Hymenophyllum polyanthos* (Swartz) Swartz. Many, but by no means all, of these ferns are frequent to common in Suriname. Examples of locally rare species are the *Psilotum* and also *Cheiroglossa palmata* (L.) Presl.

2. Tropical American–Tropical African Species.—These are all widespread in tropical America, and the same holds for Suriname. There are two certain examples (0.7%) of this distribution type: *Thelypteris quadrangularis* (Fée) Schelpe (see A. R. Smith, 1971) and *Xiphopteris serrulata* (Swartz) Kaulf. Two more possible examples (another 0.7%) are: *Pityrogramma calomelanos* (L.) Link, which perhaps is native in Africa, and *Trichomanes rigidum* Swartz, which is regarded by some modern authors (Taton, 1946; Schelpe, 1970) as conspecific with the African *T. cupressoides* Desv. Most examples of this distribution type recorded in the older literature have proved to be incorrect, like *Polypodium polypodioides* (L.) Watt and *Trichomanes krausii* Hook. & Grev.; the African plants are now assigned to other species.

TABLE 1. NUMBER AND PERCENTAGE OF SURINAME PTERIDOPHYTES ACCORDING TO DISTRIBUTION TYPE.

Distribution type	*Number*	*Percent*
1. Pantropic	13	4.5
2. Tropical American–Tropical African	2+2?	0.7+0.7?
3. Tropical American—Tropical Asiatic	2	0.7
4. Neotropic-wide	104	36.5
5. Tropical Continental American	19	6.7
6. Tropical (and Subtropical) South American	23	8.0
7. Northern South American	56	19.7
8. Circum-caribbean	23	8.0
9. Northern South American—Lesser Antillean	12	4.2
10. Guianan-wide Endemic	7	2.3
11. Restricted Guianan Endemic	8	2.8
12. Anomalous	12	4.2
13. Alien	3	1.0
	286	100.0

3. Tropical American–Tropical Asiatic Species.—Some of these extend to tropical Australia. There are two examples (0.7%) in Suriname: *Blechnum serrulatum* L. C. Rich. and *Pteridium aquilinum* (L.) Kuhn subsp. *caudatum* (L.) Bonap. Both are terrestrial species of open habitats.

4. Neotropic-wide Species.—These occur almost throughout tropical America, except for the driest and loftiest parts, and in many cases extend to Florida, subtropical Brazil, Argentina, etc. This is by far the largest group, and includes 104 (36.5%) species. Slightly over a third of these are epiphytes, a figure that comes very close to the proportion of epiphytes in the Suriname pteridophyte flora as a whole. Examples can be gleaned from the forthcoming Flora.

This group may actually be too large. Some species may have been too broadly circumscribed and may eventually be shown to consist of several smaller, less widespread species, as Evans (1969) has demonstrated for *Polypodium pectinatum* L. *sensu latissimo*.

There seems to be little correlation between the size of the area of a species and its frequency in Suriname. Some neotropic-wide species are very common, like

Adiantum latifolium Lam. and *Ctenitis protensa* (Afz.) Ching. But others, like *Cyclopeltis semicordata* (Swartz) J. Smith and *Doryopteris pedata* (L.) Fée, are quite rare.

5. Tropical Continental American Species.—A few of these species extend to Cuba and/or to Jamaica, islands known to have a fair share of otherwise continental neotropical species. Trinidad is here regarded as part of the continent, for geological and general biogeographical reasons.

Nineteen species (6.7%) exhibit this kind of distribution, in my opinion a surprisingly low figure. Examples are: *Adiantum humile* Kunze, *Lindsaea divaricata* Klotzsch, *Metaxya rostrata* (H.B.K.) Presl, *Polypodium percussum* Cav., *Selaginella flagellata* Spring, and *Trichomanes botryoides* Kaulf. Only three or four of the group are epiphytes.

6. Tropical (and Subtropical) South American Species.—Some of these extend to Panama, and many to Trinidad. There are 23 species (8%) in this group. Examples are: *Adiantum dolosum* Kunze, *Anemia villosa* Humb. & Bonpl. ex Willd., *Dicranoglossum desvauxii* (Klotzsch) Proctor, *Oleandra pilosa* Hooker, *Polypodium (Microgramma) persicariifolium* Schrad., *P. decumanum* Willd., *Selaginella radiata* (Aubl.) Spring, and *Thelypteris hostmannii* (Klotzsch) Morton. Nine are epiphytes.

7. Northern South American Species.—These sometimes extend into Panama and/or Trinidad. Most occur only in the Guianas from Amapá westward and range to Venezuela and eastern Colombia, but several extend to Amazonian Peru and/or Brazil, approximately to the Amazon River. This is a large group of 56 species (19.7%). Surprisingly, only seven epiphytes show this type of distribution. Typical examples of terrestrial species include *Adiantum leprieurii* Hooker, *Ctenitis refulgens* (Klotzsch) Vareschi, *Doryopteris conformis* Kramer & Tryon, *Lindsaea parkeri* (Hooker) Kuhn, *Lycopodium duidae* A. C. Smith, *Selaginella parkeri* (Hook. & Grev.) Spring, *Thelypteris macrophylla* (Kunze) Morton, and *Trichomanes cellulosum* Klotzsch. Examples of epiphytic species are: *Elaphoglossum laminarioides* (Bory) Moore, *Grammitis furcata* Hook. & Grev., *Trichomanes pinnatinervium* Jenm., and *Xiphopteris nana* (Fée) Copel. The latter is reported to extend to Mato Grosso, Brazil.

8. Circum-caribbean Species.—This designation is not entirely correct, as the species extend, of course, far to the east of the Caribbean Sea into the Guianas. Under this heading I have assembled the species occurring in the West Indies (and more or less throughout them), Central America, and northern South America from Colombia to Suriname, French Guiana, or Amapá. A few extend south to Peru or north to the southeastern United States; others have only been recorded from some scattered localities in the area and perhaps will eventually prove to have a more continuous distribution pattern.

This is an interesting distribution type, of which I have found few examples in recent literature. Van Donselaar (1965, p. 75ff, table 11) made an analysis of the distribution of savanna plants in Suriname. He did not explicitly distinguish a circum-caribbean element, but his table includes some instances of this distribution type: *Montrichardia arborescens* (L.) Schott (Araceae), *Heliotropium*

fruticosum L. (Boraginaceae), and *Rhynchospora curvula* Griseb. (Cyperaceae). Thomas's map (1960, p. 79) of *Cyrilla racemiflora* L., when supplemented by some finds in Suriname, comes close to this distribution type. Tryon (1972) analyzed the concentration of endemic ferns in the neotropics, distinguishing centers of endemism and floristic connections between them, but did not come across this particular distribution pattern.

There are no fewer than 23 pteridophytes (8%) in this category; perhaps a few of these have insufficiently known distributions that extend further, and so do not really belong here. It seems highly significant that 15 of the species are epiphytes, and that the great majority of the species occur in Suriname only in the hills and mountains. Two Guianan Gesneriaceae have this distribution type: *Chrysothemis pulchella* (Donn ex Sims) Dcne. and *Columnea scandens* L. (Leeuwenberg, 1958, map 1), but only the latter is an epiphyte. I should be grateful to have further examples of pteridophytes or other plants brought to my attention. The circum-caribbean distribution type must have a paleogeographical-ecological basis. What is so striking about it is that the species do not extend all the way south along the Andes to Bolivia and in the Brazilian coastal ranges to southeastern Brazil, as a good many other species do.

Examples of circum-caribbean pteridophytes in Suriname are *Ceratopteris deltoidea* Bened., *Cochlidium linearifolium* (Desv.) Maxon in C. Chr., *Hymenophyllum lanatum* Fée, *Polystichopsis ochropteroides* (Baker) Morton, *Polypodium dissimile* L., *Thelypteris decussata* (L.) Proctor, *Antrophyum feei* Schaffner ex Fée, *Ctenopteris melanosticta* (Kunze) Copel., and *Lycopodium wilsonii* Underw. & Lloyd. The last two species seem to be known only from a few scattered localities, but apparently fall into this category.

9. Northern South American–Lesser Antillean Species.—These also may extend to Puerto Rico or Hispaniola, but are absent from Cuba, Jamaica, and Central America (except for Panama in some cases). Therefore, these species cannot be called circum-caribbean. I have found 12 examples (4.2%) of this distribution type in Suriname, four of them epiphytes. Among them are: *Adiantum phyllitidis* J. Smith, *Cyathea (Nephelea) imrayana* Hooker, *Elaphoglossum pteropus* C. Chr., *Lindsaea guianensis* (Aubl.) Dryand. subsp. *guianensis*, *Ormoloma imrayanum* (Hooker) Maxon, which has not yet been recorded from Suriname but which is known from both French Guiana and Guyana (formerly British Guiana), *Thelypteris glandulosa* (Desv.) Proctor, and *Trichomanes pedicellatum* Desv.

10. Guianan-wide Endemic Species.—These are not strictly confined to the Guianas, but often range south and east to the territory of Amapá, Brazil, and northwest to the territory of Delta Amacuro, Venezuela, and to Trinidad. Considering that Tryon (1972) treated the Guianas as a secondary center of fern endemism, this group is surprisingly weak in Suriname, but he delimited the area more broadly than is done in the present study. Seven species (2.3%), two of them epiphytes, are included in this group. According to Tryon, the Roraima sandstone substrate is important for the occurrence of Guianan endemics. This substrate is very limited in Suriname, and consequently the species occurring on it are neither widespread nor richly represented in the country. The Guianan endemics of

Suriname enumerated below actually are not at all sandstone species. I should like to emphasize that species representative of the sandstone flora, like *Lindsaea pendula* Klotzsch, occur in the whole Roraima sandstone area from Suriname to southeastern Colombia, and are here classified as species of northern South America (group 7), not as Guianan-wide endemic species. The species of this group are: *Adiantum adiantoides* (J. Smith) C. Chr., *Cyathea boryana* (Kuhn) Domin, *Danaea trifoliata* Reichenb. in Kunze, *D. simplicifolia* Rudge, *Elaphoglossum luridum* (Fée) Christ, *Stigmatopteris varians* (Fée) Alston, and *Thelypteris guyanensis* (Fée) Morton. I would like to be informed whether any of these species occur in other areas, unknown to me.

11. Restricted Guianan Endemic Species.—The Guianan area is defined as for group 10. With more complete data, the subgroups herein may prove to coincide, or at least to blend with one another. The eight species (2.8%) in this category may be grouped as follows.

a. Suriname and French Guiana (and Amapá): *Trichomanes mougeotii* v. d. Bosch and *Ctenopteris kegeliana* (Kunze) Kramer.[2]

b. Suriname and Guyana: *Cyathea (Sphaeropteris) marginalis* (Klotzsch) Domin.

c. Suriname only: *Adiantum tripteris* Kramer, *Ctenopteris staheliana* (Posth.) Kramer,[3] *Notholaena solitaria* R. M. Tryon, *Selaginella caudorrhiza* Baker, and *Thelypteris holodictya* Kramer. Because the taxonomic status of *Ctenopteris staheliana* and *Selaginella caudorrhiza* is open to some doubt and because the other species have all been found only once and therefore hardly anything is known about their distribution, we certainly may not call Suriname a center of fern endemism.

12. Anomalous Species.—These have unusual distribution types, at least as far as ferns are concerned, and hardly are suitable for qualitative evaluation. Again, further exploration may show some of them to have other, more usual distribution patterns. Others will, however, probably remain "anomalously" distributed, as is found occasionally in phytogeography (see van Balgooy, 1971, pp. 71–73). The 12 species (4.2%) may be grouped as follows.

a. Suriname and low-lying areas along the coast of eastern and southeastern Brazil: *Elaphoglossum strictum* (Raddi) Moore.

b. Northern South America–southern Brazil disjuncts: *Doryopteris sagittifolia* (Raddi) J. Smith, *D. collina* (Raddi) J. Smith, and *Stigmatopteris rotundata* (Willd.) C. Chr. This type of distribution occurs in several *Doryopteris* species and was discussed by Tryon (1944). Examples among angiosperms also exist: *Habenaria platydactyla* Kraenzl. (Orchidaceae) and *Psidium grandifolium* Mart. (Myrtaceae).

c. Central and northern or northwestern South America, but not extending throughout Central America (including southeastern Mexico) and tropical South America. This distribution is a fragment of group 5. The species that have this

[2]Ctenopteris **kegeliana** (Kunze) Kramer, comb. nov. Basionym: *Polypodium kegelianum* Kunze, Linnaea **21:** 210. 1848.

[3]Ctenopteris **staheliana** (Posth.) Kramer, comb. nov. Basionym: *Polypodium stahelianum* Posth., Rec. Trav. Bot. Néerl. **23:** 401, f. 2. 1927.

type of distribution are: *Diplazium lechleri* (Mett.) Moore, *Polypodium adnatum* Kunze, *P. flagellare* Christ, and *Trichomanes tuerckheimii* Christ. In connection with what was said under group 8, it may be significant that all these species except the *Diplazium* are epiphytes.

d. West Indian and tropical South American species apparently lacking in Central America. None of these are epiphytes: *Lomagramma guianensis* (Aubl.) Ching, *Pteris deflexa* Link, and *Tectaria trifoliata* (L.) Cav.

13. Alien Species.—As is the rule in pteridophytes, these are very few in number. The three species (1%) are all paleotropical or paleosubtropical in origin: *Pteris vittata* L., *P. tripartita* L., and *Thelypteris opulenta* (Kaulf.) Fosb. Because *P. tripartita* has been found in the deep south of Suriname and because I have also seen a specimen from French Guiana collected about 140 years ago, I think this species may be native but locally very rare in South America, as the preponderantly Asiatic fern *Lindsaea ensifolia* Swartz is in tropical Africa.

It may be noted in passing that out of 13 species of *Selaginella* found in Suriname, one is distributed over tropical Central and tropical South America, three over tropical South America, and eight occur only in northern South America. The doubtfully endemic *S. caudorrhiza* Baker is referred to above. It must certainly be significant that in this genus, with its much heavier spores, there are on the one hand no very widely distributed species, but on the other hand hardly any very narrowly distributed ones, although such species certainly exist in other areas. Curiously, many species extend throughout the Lesser Antilles (Alston, 1952), but none of the Guianan species reaches these islands, nor vice-versa.

RELATIONSHIPS AND HISTORY OF THE SURINAME PTERDIOPHYTE FLORA

In the older literature (e.g., Christ, 1910, pp. 301–303) and more recently, in papers dealing mainly with forest trees and their distribution, the flora of the Guianas often is treated as an appendix, as an offshoot of the flora of Amazonian Brazil. This seems unlikely on geological–paleogeographical grounds, and it is not at all true for an old group like the ferns, as shown above.

Another matter to be taken into account is the assumption of some authors that most of the forest cover of Suriname and larger adjacent parts of northern South America is of quite recent origin. On palynological grounds, van der Hammen (1972) showed that the cool periods of the Pleistocene were considerably drier in the area under consideration and that savannas, savanna woods, and the like were more extensive in that period than they are now. Haffer (1969) reconstructed forest refugia and corridors of migration for dry environment species, chiefly on ornithological evidence. Hoogmoed (1973) went further, stating: "...We may assume that about 3000 years ago the greater part of Suriname was covered with savannahs and that only the Tumuc Humac and Boundary Mountains were covered with rain-forest... After this dry period the forest again spread over Surinam starting from the Tumac Humac and Boundary Mountains." Ferns probably are not the best indicators of such developments in the past, and the distribution of savanna species may be much more readily explained by assumptions like Haffer's. It seems to me, however, that Hoogmoed's "deforestation" of

virtually all of Suriname until about 3000 years ago goes too far. Today the forest flora is rich in both woody and herbaceous species in areas like Tafelberg, the Emma Range, and especially Brownsberg, a surprisingly rich hill situated not very far from the margin of the coastal plain and justly proclaimed a natural reserve (Bubberman et al., 1970).

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REVIEW

"THE PHYLOGENY AND CLASSIFICATION OF THE FERNS," edited by A. C. Jermy, J. A. Crabbe, and B. A. Thomas. xiv + 284 pp. 1973. Academic Press, London and New York. 9.00 pounds; $25.00.—This volume is a pteridological banquet, albeit an expensive one. The fare is generally good, or at least provocative, although I must confess that some of the phylogenetic speculation left me with indigestion. The book is the outgrowth of a symposium held in London in 1972 and jointly sponsored by the British Pteridological Society and the Linnaean Society of London. Individual papers fall about equally into two categories: review articles and articles presenting new research and ideas on specific groups. The latter are of most interest to me, while the former are likely to be more appreciated by a general audience.

It is fitting that this volume begins with an address by R. E. Holttum, who perhaps has had more influence on fern systematics than anyone else in the past 25 years. In a penetrating statement on the causes of our difficulties as taxonomists, Holttum reminds us that human limitations and imperfect communication are often the chief roadblocks to advancing taxonomy. Pichi Sermolli, in a lavishly illustrated paper, then painstakingly reviews the incremental changes in fern classification since the beginning of taxonomic time. There follow papers by Van Cotthem (stomatal patterns), Atkinson (gametophytes), Swain and Cooper-Driver (biochemistry), and T. Walker (cytology) assessing the application of their respective specialties to taxonomy of ferns. Walker also includes several new and intriguing chromosome reports while focusing on where cytology is most likely to produce added insight into taxonomic problems. Bierhorst expands upon his theory of the origin of the fern leaf, using as examples the non-appendicular fronds of his favorite organisms, *Stromatopteris* and *Psilotum*, as well as several other "primitive" genera. There is a short, almost perfunctory paper by Harris on fossil ferns. One gets the impression that there is either little to add to the subject since publication of an earlier symposium on the origin and evolution of ferns (Mem. Torrey Bot. Club **21**(5):1-95. 1964) or that there is a distressing lack of communication between pteridologists and paleobotanists (need they be mutually exclusive?), a state of affairs hinted by Manton in her closing address.

The coverage of individual groups of ferns is necessarily incomplete but broad. Mickel tackles the dennstaedtioid ferns but comes up nearly empty-handed, concluding that we don't yet know enough to assess their relationships. Working from a broader data base, Holttum offers his views on the origin of the thelypteroid ferns and suggests possible cyatheoid ancestry. His analysis was possible only after extensive monographic work that he himself conducted on Old World

Thelypteridaceae. Herein lies to me the most important lesson of this symposium volume: phylogenists are largely at an impasse until modern monographic treatments are available for critical groups. This is especially necessary for the evolutionarily pivotal dennstaedtioid ferns, as Mickel and Holttum state. Reasons for the paucity of recent monographs are not discussed, but need to be. The principal reasons seem to be funding priorities and the incompatibility of the publish-or-perish cloud under which most monographers must work and the time required for successful completion of monographs.

Two of the more interesting and stimulating papers, not on the original program but happily inserted into the symposium volume, deal with spore morphology in cheilanthoid and thelypteroid ferns, by Tryon and Tryon and by Wood, respectively. Both surveys utilize the scanning electron microscope and suggest insights into classification of these groups. Undoubtedly there will be a proliferation of such surveys in the near future, it is to be hoped in a taxonomic context such as these two.

Familial boundaries of Aspidiaceae and Davalliaceae are examined by Sledge and by Sen and Sen, respectively. Sledge concludes that there is no justification for recognizing Athyriaceae as a separate family, while Sen and Sen advise against splitting off Oleandraceae from the Davalliaceae. The latters' arguments and conclusions, based on anatomical evidence from seven species in three genera, are, however, a little like deciding that Leguminosae is a good family after examining only *Mimosa, Pisum,* and *Caesalpinia*. Assignment of family rank has always been and will probably continue to be a subjective decision, arrived at by noting rank assigned to related groups. The important point is to be able to say that genera within Davalliaceae *s. l.* are more closely related to each other than to anything else, a point for which Sen and Sen do have good evidence.

There are two new phylogenies (Holttum, Mickel) and one new classification (Wagner) presented by contributors. Differences among these schemes are more striking than similarities. These schemes are offered primarily as reference points for discussion and for the purpose of testing hypotheses and promoting additional insight into relationships. Those who would rush to adopt one of these should recognize that there is no unanimity among pteridologists with regard to classification and phylogeny of ferns. There does seem to be a growing feeling that schizaeoid ferns gave rise to the gymnogrammoid–cheilanthoid line, and that Ophioglossaceae and Marattiaceae have little to do with each other or with leptosporangiate ferns. We are left with several "mini" evolutionary lines, truncated at their bases. This may be less picturesque, but it is more honest, in view of how little is known about the ancestry of ferns.

The volume is well-edited, with pleasing typography and good photographic reproduction. The editors have provided an index and cross-indexing. One regrets that it was not possible to capture in the book some of the undoubtedly lively discussion following some of the papers. This would have provided an appropriate dessert.—*Alan R. Smith, Herbarium, Dept. of Botany, University of California, Berkeley, CA 94720.*

SHORTER NOTES

THE STATUS AND COMPOSITION OF ASPLENOSORUS.—In 1937 Dr. Wherry established the hybrid genus *Asplenosorus* for Scott's Spleenwort, *A. ebenoides*, the hybrid between *Asplenium platyneuron* and *Camptosorus rhizophyllus*. The hybrid generic name was also used for the rare *A. inexpectatum* E. L. Braun ex Friesner (*Asplenium ruta-muraria* × *Camptosorus rhizophyllus*) in 1940.

Mr. Morton has noted (Amer. Fern J. **46**: 152–155) that there are other hybrids of the Appalachian Aspleniums that possess genomes of both *Asplenium* and *Camptosorus* that could be placed in the hybrid genus. He did not make the new combinations on two grounds. First, the International Code of Botanical Nomenclature at that time required that all new names, including hybrids, be accompanied by a Latin description or diagnosis, which *Asplenosorus* was not; therefore it was illegitimate. Secondly, Mr. Morton felt that the hybridization indicated closer relationship between *Camptosorus* and *Asplenium* than generic distinction might warrant, and so he preferred to combine the two genera.

More recently, however, the International Code (1972) has been amended to allow hybrid generic names to be validly published if the parental genera are cited (Article H.9). The following new combinations are necessary whenever *Camptosorus* is maintained as a genus distinct from *Asplenium*:

Asplenosorus gravesii (Maxon) Mickel, comb. nov.
Asplenium × *gravesii* Maxon, Amer. Fern J. **8**: 1. 1918.
Asplenium bradleyi × *Asplenium pinnatifidum*.

Asplenosorus kentuckiensis (McCoy) Mickel, comb. nov.
Asplenium × *kentuckiense* McCoy, Amer. Fern J. **26**: 104, *t. 11*. 1936.
Asplenium pinnatifidum × *Asplenium platyneuron*.

Asplenosorus pinnatifidus (Nutt.) Mickel, comb. nov.
Asplenium pinnatifidum Nutt. Gen. No. Amer. Pls. **2**: 251. 1818.
Asplenium montanum × *Camptosorus rhizophyllus*.

Asplenosorus trudellii (Wherry) Mickel, comb. nov.
Asplenium × *trudellii* Wherry, Amer. Fern J. 15: 49, *t. 4, f. 4–5*. 1925.
Asplenium montanum × *Asplenium pinnatifidum*.

John T. Mickel, New York Botanical Garden, Bronx, NY 10458.

TWO ADDER'S-TONGUES NEW TO MISSOURI.—For the past four years the senior author has been studying the distribution of the five species of *Ophioglossum* native to Louisiana (*O. crotalophoroides, O. engelmannii, O. nudicaule* var. *tenerum, O. petiolatum*, and *O. vulgatum* var. *pycnostichum*). After extensive searches the authors have collected two of these species, *O. crotalophoroides* and *O. petiolatum*, in southern Missouri. Both collections are state records and represent the northernmost known locality for each species.

Ophioglossum crotalophoroides Walt., Bulbous Adder's-tongue, was found on a south-facing slope in sandy, cherty soil in Thayer City Cemetery in Oregon County, Missouri, on April 12, 1974 (*Thomas et al. 38497*). Ninety-two small plants were collected in three different areas of the recently developed part of the cemetery. None were found in the Bluegrass sod of the older part of the cemetery. Many of the specimens were fertile, but all were smaller than those from the southern part of the United States. This fern is easily overlooked, and two collecting trips to this spot on rainy days in April, 1973 were fruitless.

Ophioglossum petiolatum Hooker, Stalked Adder's-tongue, was collected in sandy soil beside the south wall of Holly Grove Baptist Church in Cooter, Pemiscot County, Missouri, on May 15, 1973 (*Thomas & Marx 34700*). The reflected heat from the building probably helps to keep the soil warm enough for this fern to become established.

Voucher specimens are on deposit in the herbaria of Northeast Louisiana University and the Missouri Botanical Garden. The research was supported in part by two NLU Faculty Research Grants.—*R. Dale Thomas, Paul S. Marx, and David Lawson, The Herbarium, Biology Department, Northeast Louisiana University, Monroe, LA 71201.*

LYCOPODIUM CERNUUM IN GEORGIA'S COASTAL PLAIN—The Nodding Club-moss is common in both the New and Old World tropics. In the continental United States it grows in coastal plain areas west to Lousiana (J. K. Small, Ferns of the Southeast, 1938; E. T. Wherry, The Southern Fern Guide, 1964). In Georgia *L. cernuum* is reported from only six counties: Charlton, Brantley, Randolph (R. McVaugh and J. H. Pyron, Ferns of Georgia, 1951); Lowndes (E. Quarterman, Amer. Fern J. **43**: 73. 1953); Colquitt, and Long (W. H. Duncan, Amer. Fern J. **45**: 9. 1955; **55**: 146. 1965). The few collections of *L. cernuum* presumably reflect an uncommonness or rareness of the species in the state. Our data indicate a broader range than previously thought and suggest a more general occurrence of *L. cernuum* in Georgia.

We now wish to report a northward range extension of roughly 60 miles and seven new county records in Georgia's coastal plain. The new localities with voucher specimens are BRYAN CO.: Borrow pit near the Ogeechee River and US-80, *Drapalik & Jacobs 2368* (MICH, NCU, Georgia Southern College); BULLOCH CO.: Borrow pit along unpaved road six miles south-southwest of Statesboro, *Bruce & Drapalik 72045* (MICH); CANDLER CO.: Borrow pit 11 miles west-northwest of Statesboro, *Bruce & Drapalik 72058* (MICH); ECHOLS CO.: Borrow pit 1.2 miles north of Howell along Ga-135, *Norsworthy 340* (Valdosta State College); GRADY CO.: Roadside bank two miles south of Whigham, *Faircloth 4* (GA, Valdosta State College); MCINTOSH CO.: Three miles from Long County line on Ga-99, *Newton 63* (Georgia Southern College); and WAYNE CO.: Borrow pit on edge of Satilla River flood plain southwest of Screven, 9 Dec 1973, *Waters s. n.* (Valdosta State College).

In Georgia *L. cernuum* inhabits sandy-clayey areas which are relatively open and moist. Known sites are man-made disturbed places, most often borrow pits and road cuts.

These new county records more than double the number of reported localities for the state of Georgia. In addition, the Bryan, Bulloch, and Candler County sites show *L. cernuum* to exist at a latitude further north than the southern-most portions of South Carolina where it has not yet been found.—*James G. Bruce, Donald J. Drapalik, and Wayne R. Faircloth; Department of Botany, The University of Michigan, Ann Arbor, MI 48104; Department of Biology, Georgia Southern College, Statesboro GA 30458; and Department of Biology, Valdosta State College, Valdosta, GA 31601.*

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ERRATA FOR 1974

P. 3, line 17. For "*Fig. 6*" read "*Fig. 7.*"
P. 3, line 18. For "*Fig. 7*" read "*Fig. 4.*"
P. 4, legend. FIG. 4 is *H. levyi* and FIG. 7 is *H. pinnatifida.*

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P. 28, plate. Reverse "1B" and "2B."
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Cheilanthes in Florida[1]

A. MURRAY EVANS*

In working with the pteridophytes of the southeastern United States as part of the Southeastern Flora Project, I found some specimens of note in the genus *Cheilanthes* in the University of Florida Herbarium (FLAS).

One collection is stamped as a "Gift of Robert P. St. John," with label data "#284, Nov. 28, 1934, from wooded rock hill near Lecanto, Florida" (presumably Hernando County). This specimen has gone under the name *C. microphylla* Swartz, but is *C. lanosa* (Michx.) D. C. Eaton. This is the only collection of this species I have seen from Florida. The nearest station I know of is in Coffee County, Georgia, some 200 miles north. Several other FLAS specimens collected at Lecanto, however, are *C. microphylla*. The "wooded rocky hill near Lecanto" with which I am familiar is the so-called "Lecanto grottoes," now an open, pastured woods pitted with limestone outcrops and small sink holes about ten miles northeast of Brooksville along county road S491A. I have not seen either species of *Cheilanthes* there on any of several visits over the past ten years, but that does not mean that they might not be there or in another outcrop area in that region. It would be of interest to know if either species still occurs there, and particularly if other new stations for *C. lanosa* exist. I can only assume that the St. John specimen of *C. lanosa* is not a mixed label of this normally more northern plant. The label and habitat data do fit, and it is likely that this species would grow on dry, limestone outcrops such as these.

There also are several collections of *Cheilanthes* from near Chipley, Washington County, at "Cedar Grove," also on limestone rocks, collected by J. K. Small, E. West, and associates between 1934 and 1937. These are depauperate specimens of *C. microphylla* which resemble *C. alabamensis* (Buckl.) Kunze somewhat. However, they are more hirsute than *C. alabamensis* and have 64 spores per sporangium, which I find consistent with other specimens of *C. microphylla* from Florida and Jamaica. *Cheilanthes alabamensis* is apogamous, with 32 spores per sporangium. These depauperate collections from the northern edge of the range of the species in many ways parallel the depauperate collections of *Polypodium dispersum* Evans commonly encountered at the northern extremities of its range, such as those from the limestone outcrops at Buzzard's Roost in Alachua County, Florida.

There is an additional collection of *Cheilanthes* from Matheson Hammock, Miami, Dade County, collected by E. S. Ford in 1963. This is a depauperate collection from a residential development area. It was tentatively identified as *C. microphylla*. However, Knobloch (Amer. J. Bot. **54**: 462. 1967) questioned its identity and suggested that it might be a hybrid or an as yet undetermined West Indian species. Although Knobloch indicated univalents at meiotic metaphase for this collection, both this and his other collection of *C. microphylla* were counted

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*Department of Botany, University of Tennessee, Knoxville, TN 37916.

[1]Contr. Bot. Lab. Univ. Tenn. N.S. 439.

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as tetraploids with a total of 116 chromosomes. The herbarium specimen from FLAS has 64 apparently normal spores per sporangium, and so it is not likely to be of hybrid origin. I have compared this collection with specimens at the U.S. National Herbarium, and nothing is completely identical with it. Closest among the West Indian species is *C. microphylla*, but the Florida specimen is smaller, less hirsute than typical material, and the rhizome and stipe base scales are distinctly darker castaneous brown. Although open to further interpretation, this collection fits somewhat uncomfortably within the variability of *C. microphylla*. C. E. Delchamps (pers. comm.) indicated that the population still exists, and so we can hope survival will allow further clarification of the identity of this population.

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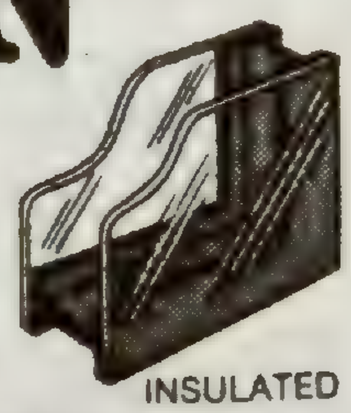

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A New Species of Lycopodium from the Peruvian Andes

CRISTINA ROLLERI *

At the beginning of my study of Lycopodiaceae from the South American Andes, a specimen was found which could not be referred to any of the taxa already known in the group. The description of this new species, with additional information on its internal morphology, distribution, and affinities, is given in this paper.

Lycopodium papillatum Rolleri, sp. nov. Figs. 1–17.

Planta terrestris vel saxicola, ca. 40 cm alta, in dimidio inferiori sterilis, superne fertilis. Caulis digitatus candelabriformis 3–4-dichotomus ca. 2–3 mm crassus erectus flexibilis saepe rubescens papillosus. Folia fertilia et sterilia isomorpha, sed fertilibus minoribus, numerosa inflexa haud adpressa non imbricata (caulibus et sporangiis parum visibilibus) in verticillis 5-foliatis disposita, ovali-deltoidea symmetrica 10.5-11 mm longa crassa, basi expansa subcuculliformia, apice acuta inflexa, papillosa, papillis numerosis conicis, supra tantum marginalibus, infra totam laminam tegentibus. Sporophylla cum area circulari papillosa basali juxta sporangium. Sporangia reniformia conspicua axillaria. Sporae tetraedro-globosae, (77)84(87) μm diametro, parte distali foveolata, parte proximali laevi.

TYPE: Cerro Malcabal (Cerro Tumbe), 3–6 km SW of Molinopampa, Amazonas Province, Chachapoyas Department, Peru, 2900 m alt, *J. J. Wurdack 1456* (US).

This species, which is as yet known only from the type material, shows evident affinities with *Lycopodium saururus* Lam. Both show the same "*L. saururus* type"[1] of growth habit and similar ecological preferences; they are saxicolous or terrestrial plants growing in high paramos or boggy areas.

Lycopodium papillatum differs from *L. saururus* in many ways. Its stems are 2–3 mm in diameter, much branched, and often reddish. Its leaves are inflexed, straight, oval-deltoid, smaller than those of *L. saururus*, distant, do not cover the sporangia completely, and are disposed in whorls of 5. Its stem and leaves bear conical, straight, and very abundant papillae. These are of such a size that it is possible to observe them with only slight magnification, and they make the leaf margins appear denticulate. The papillae occur on both faces of the leaf, but differ in their distribution: on the adaxial surface the papillae form a wide, marginal band, whereas they spread over the whole abaxial surface. The sporophylls have, in addition, a papillate area where they contact the sporangium. The leaves of *L. papillatum* lack marginal groups of mechanical cells that occur in *L. saururus* and differ from that species in the morphology of their epidermis (*Figs. 9–13*), especially in the sinuousness of the cell walls and the stomata, which are distributed over the entire abaxial surface but which are confined to a band three or four stomata wide on the adaxial surface. The spores are foveolate.

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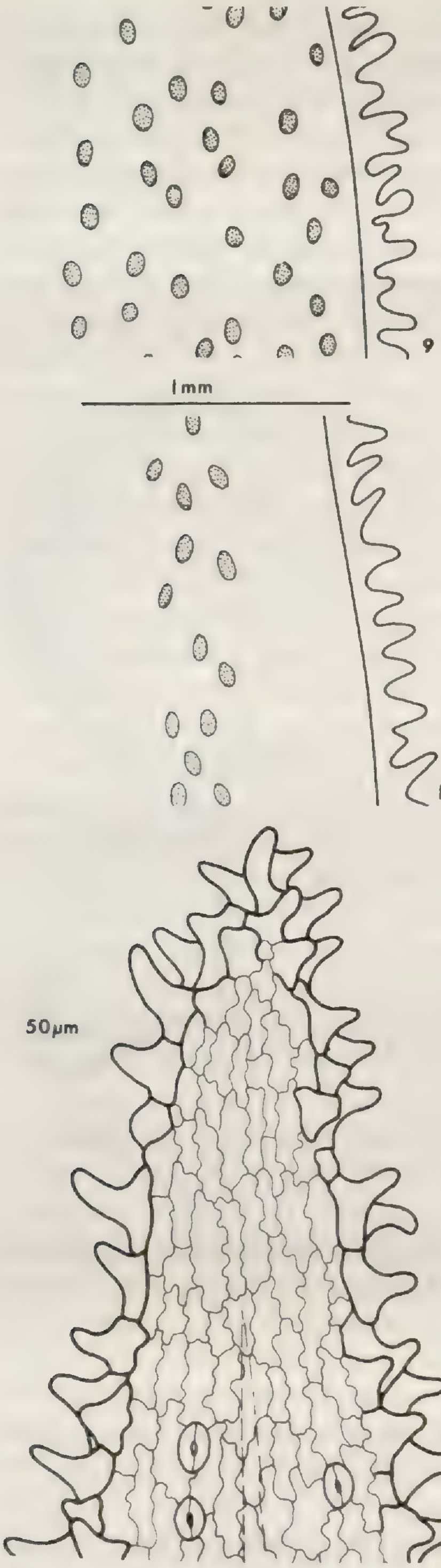
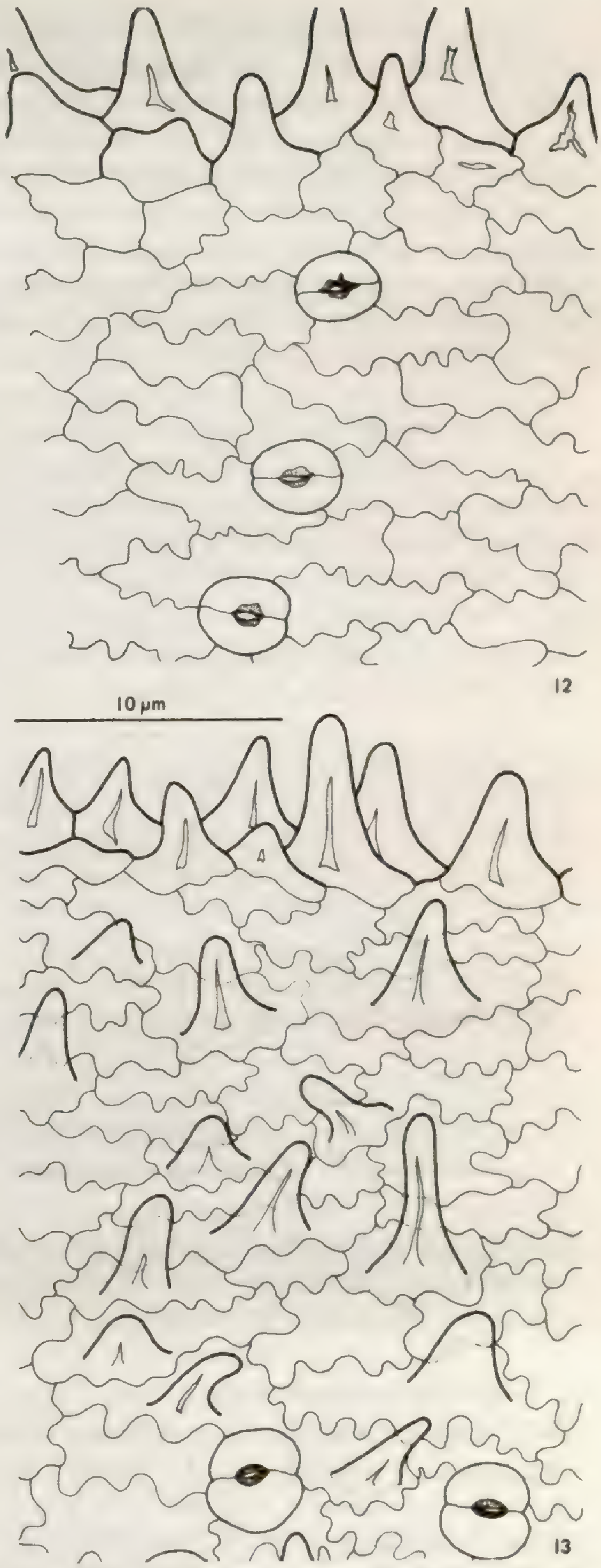
[1]Rolleri, Cristina. 1972. Morfología comparada de las especies de Lycopodium (Lycopodiaceae-Pteridophyta) del noroeste argentino. Rev. Museo La Plata n.s., **12:** 223–317.

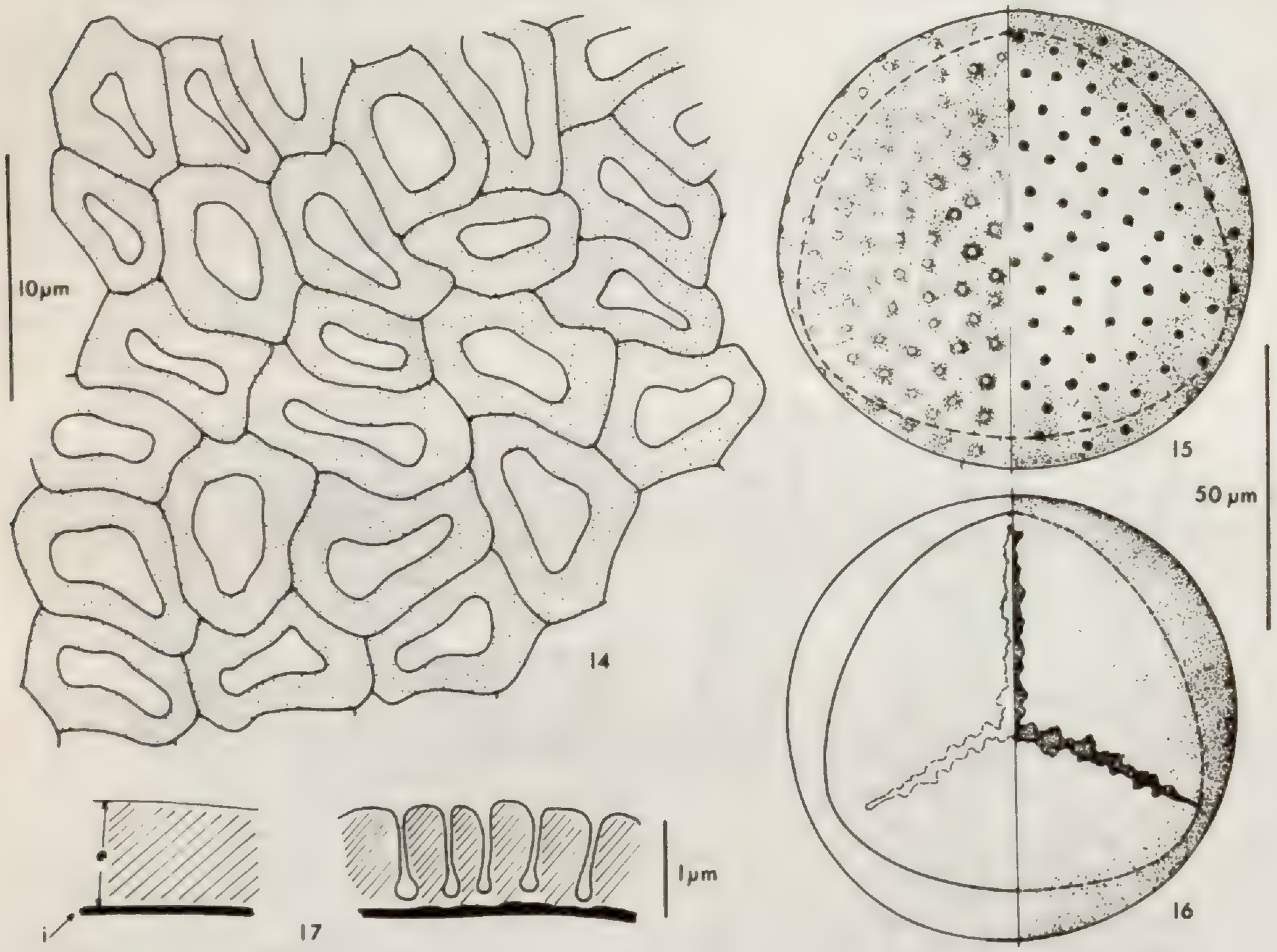
Morphology of *Lycopodium papillatum* leaves. FIGS. 1–2. Sterile leaves. FIGS. 3–5. Fertile leaves. FIGS. 6–7. Verticillate phyllotaxis with five leaves. FIG. 8. Fertile branch tip.





Anatomical details of *Lycopodium papillatum* leaves. FIG. 9. Stomata on abaxial surface. FIG. 10. Stomata in a band on adaxial surface. FIG. 11. Sterile leaf tip. FIG. 12. Epidermis of abaxial surface. FIG. 13. Epidermis of adaxial surface.

Lycopodium saururus differs in its succulent stems that are 4–5 mm in diameter, not much branched, and always green. Its leaves are adpressed, lanceolate-deltoid, cover one another and also the sporangia, and are disposed spirally with a phyllotactic fraction of 8/21. Its leaves bear many small, globoid, marginal papillae very close to each other only on the abaxial face. The leaves of *L. saururus* have marginal groups of mechanical cells formed of 3–5 rows of epidermal cells with thickened walls and conspicuous pits, sometimes fusiform, and are densely covered by small papillae. The spores are foveolate-rugulate.



Sporangia and spores of *Lycopodium papillatum*. FIG. 14. Epidermis. FIG. 15. Spore, distal face. FIG. 16. Spore, proximal face. FIG. 17. L-O analysis of spore wall showing thickness and depth of foveolae; e = exospore, i = endospore.

The morphological study and drawings of *Lycopodium papillatum* were made in the Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. David Lellinger had already observed the possibility that a new species was involved, and he encouraged me to undertake its study. Thanks are due to Elías R. de la Sota, Laboratory of Plant Morphology, Museo de La Plata, for his suggestions on and corrections to the original manuscript, and to Angel L. Cabrera, Vascular Plants Division, Museo de La Plata, for helping me with the Latin description.

An Escape Mechanism for Spermatozoids in Azolla Massulae

K. FOWLER*,[1]

The genus *Azolla* belongs to the Salviniaceae, a family of heterosporous, free-floating ferns occurring in fresh-water habitats, mainly in warm temperate to tropical regions. Stratigraphically, the genus ranges from the late Cretaceous to the present. Six living species usually are recognized. In recent years, considerable interest has been focused on fossil members (some 48 species have been recorded) which, together with the living species, are placed in six sections of the genus. The morphological and taxonomic diversity of *Azolla,* particularly of its reproductive structures, coupled with the short stratigraphic ranges of individual fossil species, renders it a potentially valuable stratigraphic indicator.

In modern species of *Azolla* sporocarps are borne in pairs which arise from the ventral lobe of the first leaf of a branch. These paired sporocarps may be of the same sex or they may be male and female, termed microsporocarp and megasporocarp, respectively. The microsporocarp contains numerous microsporangia bearing massulae; within the megasporocarp is a single megasporangium containing a megaspore apparatus. The massula and megaspore apparatus are highly distinctive structures peculiar to *Azolla*.

Probably no group of embryophytic plants has a more complex megaspore. The megaspore apparatus consists of the megaspore, above the proximal pole of which lies a superstructure of hair-like filaments called the columella. The columella, which is continuous with similar filaments on the megaspore wall, bears vacuolate, pseudocellular floats, which number three or nine in modern species. The columella and floats constitute the so-called swimming apparatus.

The massula is a pseudocellular structure in which the microspores are embedded; in living species it may be eglochidiate or may have hair-like or anchor-shaped processes called glochidia.

Interpretation of the development of reproductive structures in *Azolla* commenced many years ago (Meyen, 1836; Griffith, 1844) and has concentrated on *A. filiculoides* Lam. (Strasburger, 1873, 1889; Campbell, 1893; Hannig, 1911; Duncan, 1940; and Bonnet, 1957). *Azolla caroliniana* Willd. was studied by Berggren (1880) and by Pfeiffer (1907), *A. pinnata* R. Br. by Rao (1935), and *A. nilotica* Dcne. by Demalsy (1954). Excepting Svenson (1944), little emphasis has been placed on the taxonomic use of anatomical and morphological features of the mature reproductive structures of modern *Azolla* species.

Investigation of the reproductive structures of *A. prisca* Reid & Chandler, from the Lower Oligocene of the Isle of Wight, southern England, reveals a more

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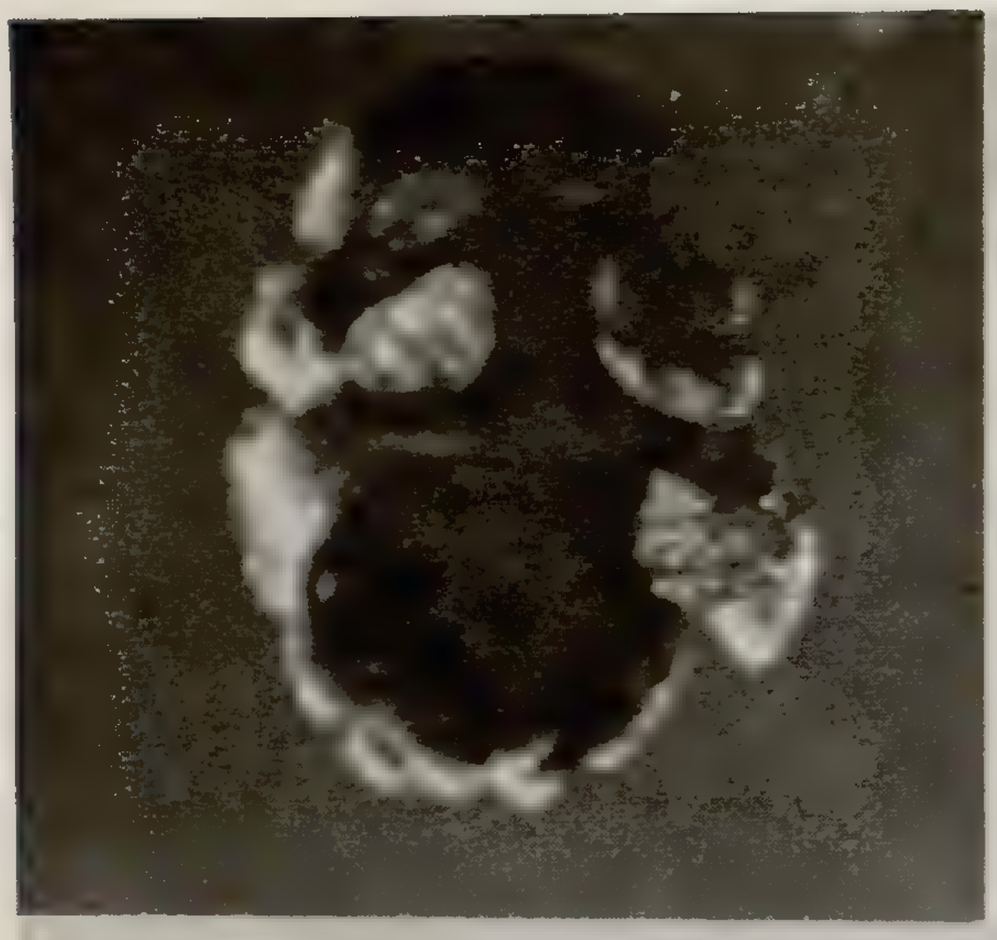
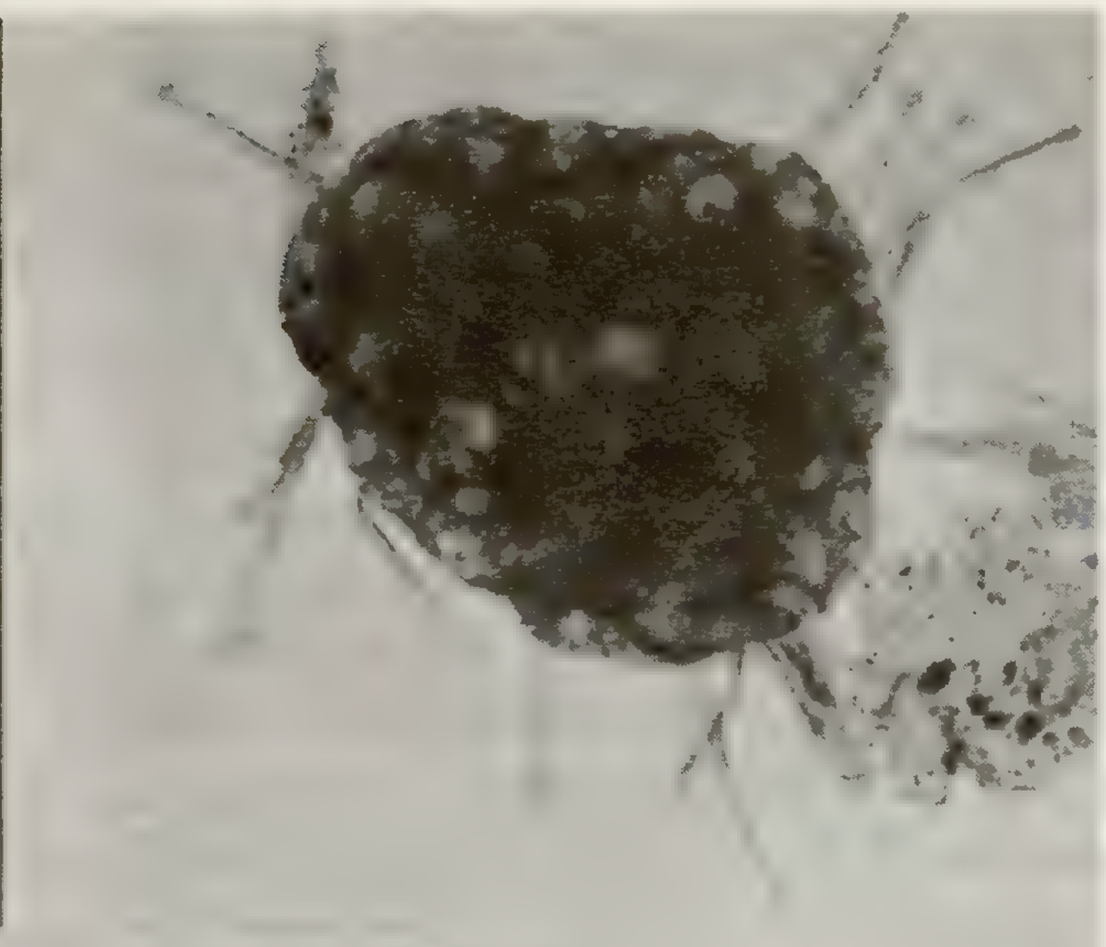
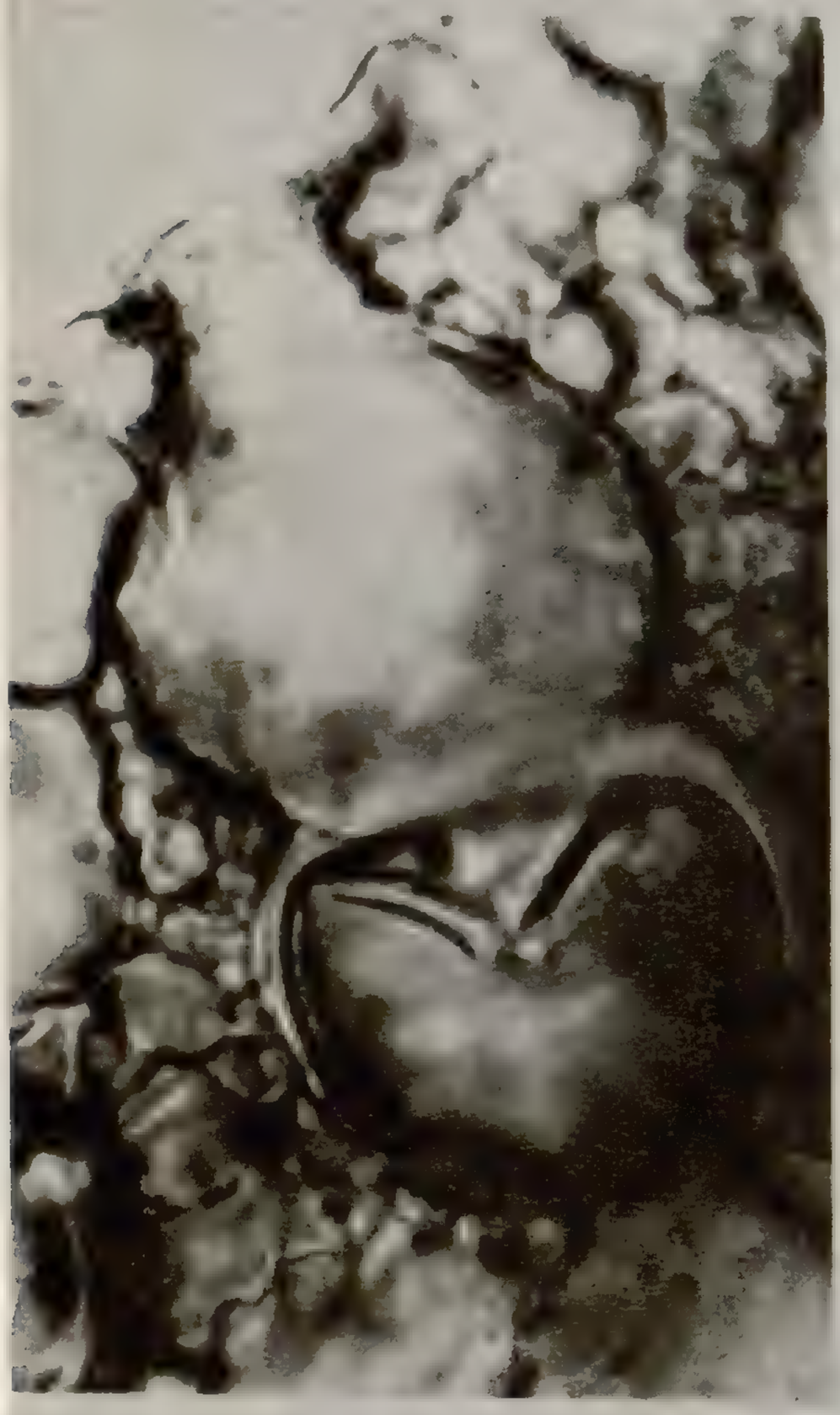
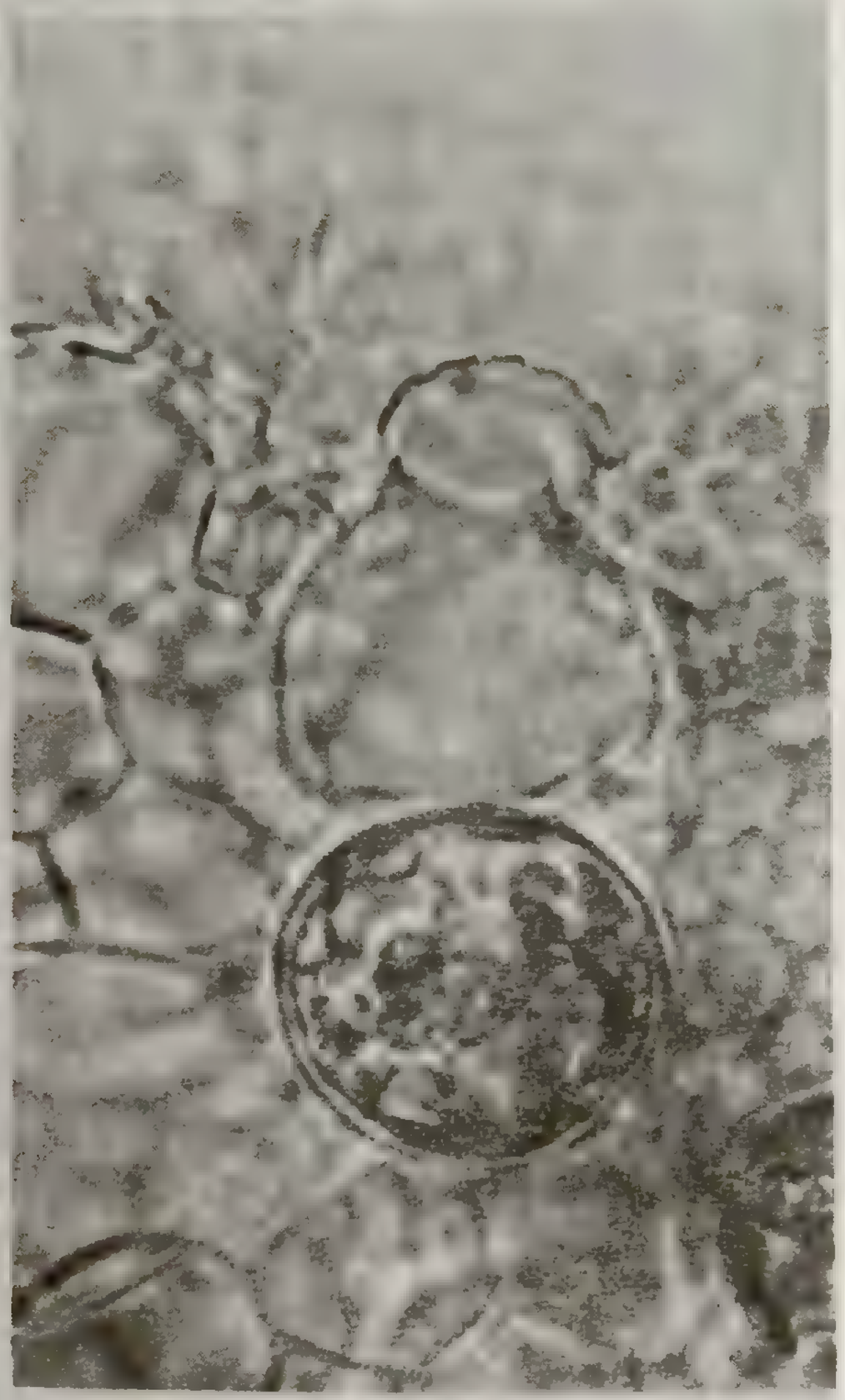
[1] I am grateful to the Keeper of Palaeontology, British Museum (Nat. Hist.) for material of *A. prisca* and to Dr. Frances M. Jarrett, Royal Botanic Gardens, Kew, and Mr. Clive Jermy, British Museum (Nat. Hist.), for material of modern *Azolla*. For his helpful advice I wish to thank Dr. K. R. Sporne, Department of Botany, University of Cambridge. Sincere thanks also to the photography section of the Department of Biological Sciences, Portsmouth Polytechnic.









FIGS. 1-3. Massula of Azolla prisca. FIG. 1. Megaspore apparatus with massula attached just below the collar region. FIG. 2. Single massula with anchor-shaped glochidia. FIG. 3. Part of massula showing a microspore-containing cavity and associated funnel-shaped cavity opening by a pore to the exterior. FIG. 4. Massula of *A. filiculoides* with funnel-shaped cavity, associated microspore-containing cavity, and microspore clearly showing cytoplasmic contents.

complex massula structure than previously supposed (Fowler, 1975). Massulae are found associated with or attached to a nine-floated megaspore apparatus; there seems little reason to doubt that both reproductive structures belong to the same species *(Fig. 1)*. The massulae attach themselves to the megaspore apparatus by means of anchor-shaped glochidia (*Fig. 2*). The glochidia are restricted to and closely adpressed to the flattened massula surfaces, and rarely project from it. Six microspores per massula is usual for *A. prisca;* each microspore occupies one of the pseudocellular cavities within the massula. Each microspore-containing cavity is closely associated with the bulbous base of a funnel-shaped cavity, the neck of which extends to the massula's periphery, and opens by a pore to the exterior (*Fig. 3*). The germinal area of the microspore, marked by a triradiate suture, consistently is positioned adjacent to the base of the funnel-shaped cavity, which often appears as a thin, incomplete partition. This association of funnel-shaped and microspore-containing cavities is a consistent feature of all massulae of *A. prisca* examined, whether the microspores have closed or open sutures. It is quite possible that the sutures may close after opening at microspore germination, giving the impression that germination has not taken place. As a result, fossil evidence can be inconclusive as to whether the funnel-shaped cavity is a primary structural feature of the massula or whether it develops after microspore germination as a result of prothallial activity. Similar structures observed in fossil massulae of *A. primaeva* (Penhallow) Arnold (Arnold, 1955) and *A. indica* Trivedi & Verma (Trivedi & Verma, 1971) have been interpreted as male gametophytes. However, in *A. prisca,* uniform, funnel-shaped cavities are associated with every microspore, including those with closed sutures. Also, the intact funnel does not appear to have been formed by the breakdown of pseudocellular material. Therefore, the funnel-shaped cavities do not appear to be the result of post-germination development of the massula. As a primary developmental feature of the massula, the funnel-shaped cavities conceivably could have been an escape mechanism for spermatozoids. But it is not likely that they develop after germination of the microspores. The only evidence that the funnel-shaped cavities may exist in the massulae of modern species of *Azolla* is provided by Campbell (1893, Plate 8, fig. 28) in an illustration of a massula containing prothallia. Eames (1936, p. 252), describing microspore germination in modern *Azolla,* states that a papilla protrudes through the opened suture, then differentiates to form a small prothallus on which an antheridium producing eight spermatozoids develops. The spermatozoids are freed by the eventual breakdown of the outer part of the massula, the gametophyte remaining embedded. Most accounts are similar, including that in Campbell (1893), and funnel-shaped cavities are not mentioned. However, examination of fresh and herbarium material of *A. caroliniana, A. filiculoides,* and its var. *rubra* (R. Br.) Strasb. reveals the presence of a similar structure and provides further evidence for considering the funnel-shaped cavity as part of the primary structure of the massula. Within the same microsporocarp, the microsporangia are seen at different developmental stages, as are the massulae. By observing developmental stages of the massula, it is seen that the funnel-shaped cavities appear as part of the developing pseudocellular structure, often before

maturity of the microspores. As a result, the funnel-shaped cavities can be found associated both with mature microspores containing cytoplasm (*Fig. 4*) and also with small, immature microspores. In both instances, the microspores clearly could not have germinated.

To the author's knowledge, no comparable structure has been recorded previously for either fossil or modern *Azolla* species. Indeed, careful and sustained observation is necessary before massula organization becomes apparent. Although germination has not been observed, it seems likely that the prothallus protrudes into the funnel-shaped exit tube, where the antheridium is developed, and the spermatozoids are released to the exterior via the pore. It is possible that similar exit tubes occur in the massulae of all *Azolla* species, both fossil and modern, but have remained undetected.

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Notes on the Polypodium vulgare Complex in South Dakota

RALPH E. BROOKS*

Throughout its range the *Polypodium vulgare* complex has been treated in various ways due to misapplied names and inadequately understood taxa. In South Dakota two members of the complex are present, *P. hesperium* Maxon and *P. virginianum* L., and both reach what may be their respective eastern and western distributional limits in central North America. The populations in western South Dakota have been referred to as a single species by some authors and as two species by others. I have determined that the western plants belong to a single species, *P. hesperium,* and that the eastern plants are *P. virginianum*. This represents the first documented report for this species in South Dakota.

Over (1932) reported that specimens from western South Dakota belonged to a single species, *P. virginianum* L. Winter, Winter, and Van Bruggen (1959) segregated the plants of that area into two species, *P. hesperium* Maxon and *P. vulgare* L. (=*P. virginianum*), but did not discuss reasons for the separation. This treatment of the western plants was altered when Van Bruggen (1967), Brooks (1969), and Petrik (1969) referred the plants to *P. vulgare* L. Van Bruggen (1972) properly recognized the western South Dakota plants as *P. hesperium*. On specimens I examined from western South Dakota, paraphyses were not present among the sporangia, which according to Lang (1972) place the plants with *P. hesperium*. At present, *P. hesperium* has been collected in Custer (*Stephens 35431 & Brooks),* Pennington (*Brooks 146 & Stephens*), and Shannon Counties (*Visher s. n.,* SDU), South Dakota.

A specimen of *P. virginianum* from eastern South Dakota was found in the University of Kansas herbarium. The label on the sheet read: "PLANTS OF SOUTH DAKOTA, *Polypodium vulgare* L., Minnihaha County: 3 miles south Garretson, Palisade Recreation Area, in crevices of Sioux quartzite outcrop, 10 July 1965, *L. Harms 2688.*" Petrik (1969) first reported this specimen but did not distinguish it from the western South Dakota plants, referring them all to *P. vulgare*. I examined the Minnihaha County collection as well as several later collections made from the same site (*Stephens 21317, Stephens 36487,* and *Brooks 1450*) and determined that the plants are *P. virginianum* L. Frequent paraphyses were observed among the sporangia on all of the specimens examined, distinguishing the plants from *P. hesperium* in western South Dakota. This was substantiated by Dr. Rolla Tryon (pers. comm.), who kindly examined a specimen (*Brooks 1450*) from Minnihaha County, South Dakota.

The Black Hills and Shannon County, South Dakota, are the only areas in the Great Plains where *P. hesperium* is known to occur. In these areas the plants normally grow in shaded crevices of granite rocks. *Polypodium hesperium* is especially frequent in areas of higher elevation in the Black Hills. The population

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of *P. virginianum* in Minnihaha County consists of about 100 plants scattered along a shaded, west-facing Sioux quartzite bluff. During my last visit to that site in 1969, the plants were in excellent condition. This site represents a western range extension for the species into South Dakota from Minnesota.

Unless otherwise indicated, all specimens referred to herein are on deposit at the University of Kansas herbarium (KANU).

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REVIEW

"BIOLOGY OF THE POTATO-FERN SOLANOPTERIS BRUNEI," by Luis D. Gómez. Brenesia **4**: 37–61. 1974.—In a taxonomic study of the primarily Costa Rican Potato Fern, Wagner (Amer. Fern J. **62**: 33–43. 1972) called attention to the few known localities of this fern and mentioned the divergent opinions regarding the function of the large, potato-like tubers (either for water retention or ant habitation). Gómez now reports six new Costa Rican localities and provides ecological, developmental, and chemical observations. Although six species of ants were found, including one species of *Azteca* that seems to be endemic to the fern, the association with ants apparently is not obligatory. The fern, however, is specialized for myrmecophily and derives definite benefits from the insects. The young tubers have a soft lid that is chewed off by the *Azteca* ants, and there are aromatic aldehydes and "sugary cells" within which attract and nourish the ants that brood in the tubers. Tubers hollowed out by the ants and sheltering them or other insects accumulate humus and debris having a high level of nitrogen and phosphorous compounds. The older, humus-filled tubers hold moisture and nutrients which are absorbed by short, thick roots of the fern that are densely covered by capitate, absorbing hairs.—*Harold Robinson, U. S. National Herbarium, Smithsonian Institution, Washington, DC 20560.*

The Effect of Coconut Milk on the Germination and Growth of Spores of Nephrolepis hirsutula[1]

CLIFFORD W. SMITH and RYLAN N. S. YEE*

The liquid endosperm of coconuts (generally referred to as coconut milk) has been used as a basal medium in many studies of the growth of angiosperm tissues. It has been used as a supplement to the medium in only a few investigations of the growth of fern tissues (Kato, 1964). Since fern tissues are relatively easy to grow in culture, there is no necessity to use supplements such as liquid coconut endosperm. However, in angiosperms the use of coconut endosperm has resulted in some very dramatic changes in the development of tissues (Steward et al., 1964). This investigation was designed to study whether or not coconut endosperm brought about any changes in the development of the gametophytes of *Nephrolepis hirsutula*.

METHODS AND MATERIALS

Spores of the Hairy Sword Fern, *Nephrolepis hirsutula* (Forst.) Presl, a common weed in drier mesic areas of Hawaii, were used in this study. The lower surface of the leaves was swabbed with 80 percent ethanol and left to dry on aluminum foil in the dark. The spores were collected, suspended in water and centrifuged at 70*g*. The sediment was resuspended in 2% Chlorox for four minutes and centrifuged. The pellet containing the spores was resuspended in sterilized distilled water and centrifuged. The washing procedure was repeated three times. The spores were inoculated onto the culture medium.

The media contained various concentrations of coconut milk diluted with deionized water. Control treatments contained Knudson's medium without or with two percent sucrose. The latter was used to detect changes in growth rate and development due to the presence of organic compounds. Any changes in growth could then be noted when studying the results of media containing coconut milk. All media were solidified with one percent agar and autoclaved at 15 p.s.i. for 20 min. Initial experiments indicated that there was little difference in the activity of liquid endosperm that had been autoclaved or filter sterilized. Twenty ml of medium was poured into 60 × 15 mm petri plates whose sides were taped after inoculation to minimize desiccation. All plates were continuously illuminated at 800 ± 100 ft-c by a bank of three cool-white fluorescent and one G.E. plant gro lights. All treatments were replicated five times and all experiments were conducted at 24° ± 1°C.

Liquid coconut endosperm was collected from coconuts of three ages. Young coconuts contained no solid endosperm and yielded 20–50 ml of liquid. Medium-aged coconuts had soft endosperm (commonly called spoon-meat) and approximately 300 ml of liquid. Mature coconuts were always collected from the ground. The peripheral endosperm was solid and the coconut contained approximately 100

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[1]A portion of this work was supported by a University of Hawaii Biomedical Sciences Support Grant.

ml of a cloudy, oily liquid endosperm.

All measurements were made using a calibrated ocular lens in a Leitz microscope. A minimum of twenty measurements were made of each replicate treatment. Standard deviations were calculated using the standard program of a Wang Model 124 Calculator.

RESULTS

Germination.—The spores germinated rapidly in Knudson's medium, producing an obvious rhizoid within 3 or 4 days of incubation. Normally 50–60% of the spores are viable. Higher viabilities can be obtained by selecting younger leaves, but the number of spores available for experiments is reduced.

When spores were cultured in various concentrations of liquid endosperm from coconuts of different ages, two effects were apparent (*Table 1*). First, spore germination was almost completely inhibited in 100% liquid endosperm from ma-

TABLE 1. PERCENTAGE OF GERMINATED SPORES OF *Nephrolepis hirsutula*.

Medium	*% coconut milk*	*7 days*	*10 days*	*15 days*	*18 days*
Young coconut milk	25	37	44	48	49
	50	34	47	46	58
	75	24	36	43	46
	100	25	31	34	28
Medium coconut milk	25	42	42	45	40
	50	11	29	28	36
	75	15	23	30	29
	100	18	20	16	17
Mature coconut milk	25	21	23	23	24
	50	6	13	24	23
	75	0	0	0	0
	100	0	0	3	2
Knudson's	0	28	44	46	58
Knudson's + 2% sucrose	0	22	32	49	46

ture coconuts. Second, with increasing concentrations of coconut milk from any source, the percentage of germinated spores decreased. This latter effect was obvious in media made from mature coconuts, but the trend also was apparent in media prepared from the younger coconuts. The apparent decline in germination of some cultures at 18 days lies within the variability of the experiments and merely represents sampling error.

Rhizoids.—Rhizoid initiation was stimulated in all concentrations of young- and medium-aged coconut liquid endosperm (*Table 2*). Mature coconut liquid endosperm concentrations above 25% were inhibitory.

Gametophyte morphology.—The effects of the various concentrations of the different liquid endosperms on the total number of cells other than rhizoids was similar to their effect on rhizoid initiation. However, the gross morphology of the gametophytes was dependent on both the concentration and age of the coconut milk (*Table 3*). The growth pattern was normal in the lower concentrations of young- and medium-aged coconut endosperm. In the higher concentrations of young- and medium-aged coconut endosperm and lower concentrations of mature

TABLE 2. AVERAGE NUMBER (± STANDARD DEVIATION) OF RHIZOIDS PER GAMETOPHYTE OF GERMINATING SPORES OF *Nephrolepis hirsutula*.

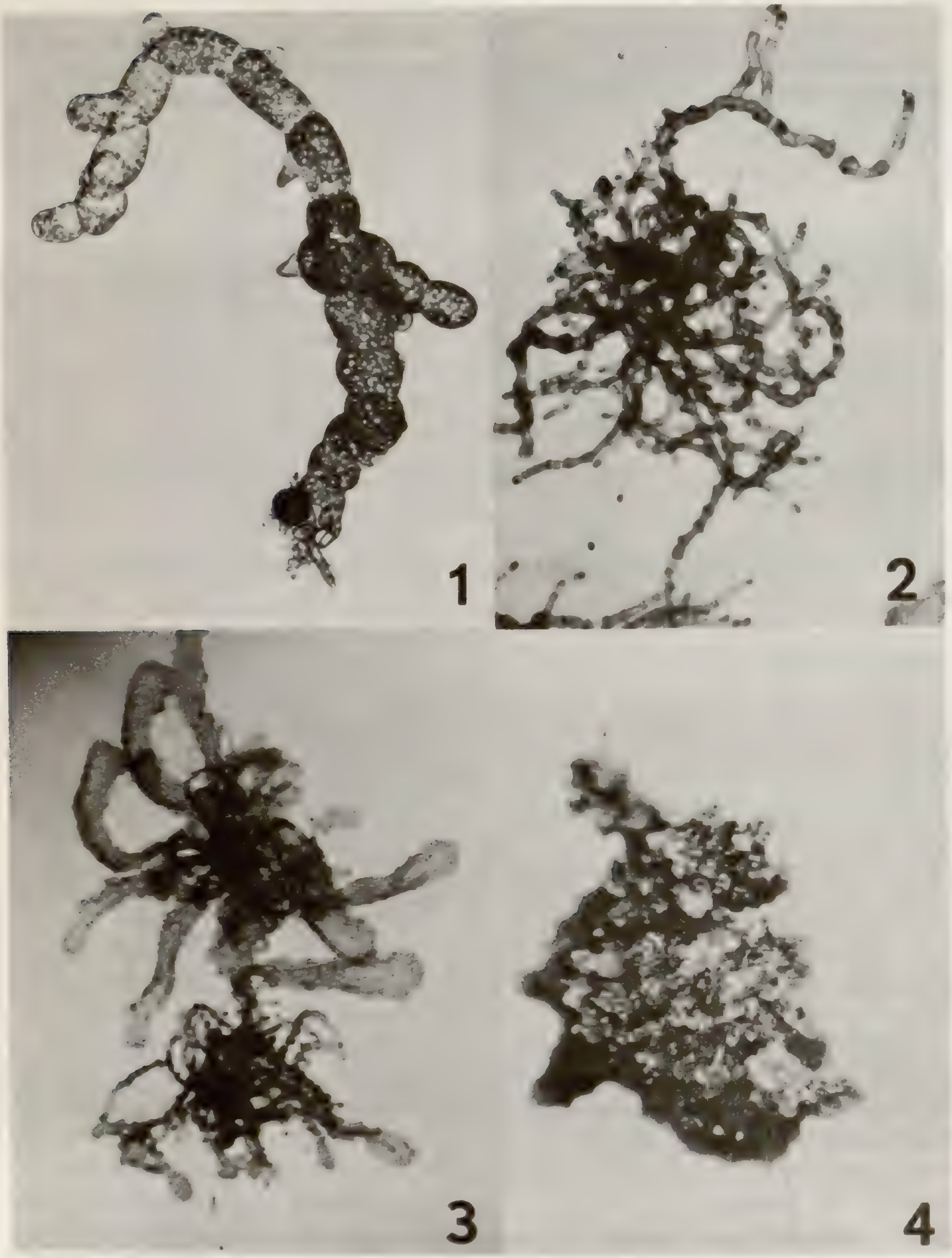
Medium	*% coconut milk*	*7 days*	*10 days*	*14 days*	*17 days*	*22 days*
Young coconut milk	25	1.0±0	1.0±0	1.7±0.7	2.4±1.3	5.2±0.4
	50	1.0±0	0.9±0.3	1.4±0.5	2.1±1.2	4.7±0.9
	75	0.8±0.4	1.0±0	1.5±0.5	1.4±0.7	3.4±1.0
	100	0	0.8±0.4	0.7±0.8	0.7±0.6	2.9±1.5
Medium coconut milk	25	0.9±0.4	1.1±0.3	2.1±0.7	2.3±0.8	5.1±1.2
	50	0.6±0.6	0.7±0.5	1.6±0.5	1.2±0.9	4.7±2.2
	75	1.0±0	0.6±0.5	0.7±0.4	1.3±0.7	3.3±1.3
	100	0	0.6±0.5	0.2±0.5	0.7±0.9	2.1±1.0
Mature coconut milk	25	0	0.2±0.5	0	1.0±0	1.5±0.7
	50	0	0	0	0	1.0±0
	75	0	0	0	0	0
	100	0	0	0	0	0
Knudson's	0	0.6±0.5	1.0±0	1.0±0	1.1±0.4	1.4±0.7
Knudson's + 2% sucrose	0	0.6±0.5	1.0±0	1.0±0	1.0±0	1.0±0

TABLE 3. LENGTH/WIDTH OF GAMETOPHYTES OF *Nephrolepis hirsutula*.

Medium	*% coconut milk*	*24 days*	*29 days*	*31 days*	*42 days*
Young coconut milk	25	3.9	2.0	1.8	1.5
	50	5.2	3.7	2.5	2.0
	75	4.3	4.7	4.1	3.9
	100	3.1[f]	1.9[f]	1.9[f]	1.9
Medium coconut milk	25	2.3	1.5	1.4	1.4
	50	4.6	3.9	2.6	1.9
	75	3.5	4.3	3.4	2.0
	100	1.5[c]	2.4[c]	1.6[c]	1.8[c]
Mature coconut milk	25	1.2[c]	1.3[c]	1.0[c]	1.0[c]
	50	1.2[c]	1.2[c]	1.2[c]	1.0[c]
	75	0	0	0	0
	100	0	0	0	0
Knudson's	0	6.2	3.8	2.8	2.0
Knudson's + 2% sucrose	0	4.4	4.7	3.9	2.7

[c] Gametophyte callus-like.
[f] Gametophyte filamentous.

coconut endosperm the gametophytes tended to grow as filaments. Generally the filaments were branched (*Figs. 1–3*), and the branching was more pronounced in the higher concentrations. If the branching was continuous, the resultant growth superficially resembled a callus (*Fig. 4*) and is referred to as callus-like in this paper. Although it is a compact tissue, it is not a true callus because the inner cells are not cemented to all their neighbors by a middle lamella because of their filamentous origin. In 25 and 50% liquid endosperm from mature coconuts only callus-like growths were produced, and there was no growth in 75 and 100%. In 75% young- and medium-aged coconut endosperm the gametophytes were a mixture of highly elongated prothalli and multibranched filaments, some of which later formed elongated prothalli (*Fig. 3*).



Photomicrographs of gametophytes grown on media containing various concentrations of liquid coconut endosperm. FIG. 1. Gametophyte after 10 days growth on 100% medium-aged coconut endosperm, ×450. FIG. 2. Gametophyte after 35 days growth on 100% young coconut endosperm, ×28. FIG. 3. Gametophytes after 35 days growth on 75% medium-aged coconut endosperm. Note the production of numerous gametophytes from the tips of some of the branched filaments, ×10. FIG. 4. Callus-like growth produced after 35 days on 100% medium-aged coconut endosperm, ×7.

Two-dimensional growth was normally established by the third week of growth. Antheridia were formed on prothalli growing on 25% young- and medium-aged coconut endosperm after growing for 7 weeks, after 8 weeks on 50% young coconut endosperm, and after 10 weeks on Knudson's medium without coconut milk. Antheridia were not observed in any other treatment. No archegonia were seen during the twelve week course of these experiments.

DISCUSSION

Although the concentrations of liquid endosperm in these experiments were higher than those normally used, the spores germinated and grew in all but the higher concentrations of mature coconut endosperm. However, the higher concentrations of endosperm from coconuts of all ages disrupted the normal development of the gametophytes. Steward and Caplin (1952) have already noted that high concentrations of liquid endosperm from mature coconuts inhibited the growth of carrot callus. It is doubtful that the abnormal growth was the result of an osmotic effect. Onion epidermis and *Spirodela* leaves did not show any signs of plasmolysis even when submerged in full strength mature coconut liquid endosperm. Also, the inhibitory effect was strongest in mature coconut endosperm and weakest in young coconut endosperm. This result is in keeping with Cutter and Wilson's (1954) observations on the growth of coconut embryos in media containing coconut endosperm of various ages. They suggested that as the coconut matured an inhibitor accumulated in the liquid endosperm.

The change in the developmental sequence in the higher concentrations of liquid endosperm is interesting. In *Nephrolepis hirsutula* the spore germinates producing a filament of four or five cells. The terminal cell then divides along the axis of the filament to initiate the growth of the two-dimensional gametophyte. The terminal cell dominates all the other cells of the filament, which become highly vacuolated soon after the establishment of the two-dimensional growth phase of the gametophyte. In *N. hirsutula* once the two-dimensional structure is established it has not been possible by means of the above experiments to convert it back to the filamentous condition. However, in high concentrations of coconut liquid endosperm the dominance of the terminal cell was suppressed, resulting in the formation of multibranched filaments. Spores grown on 50% liquid endosperm from young- and medium-aged coconuts were always two-dimensional. On 75% there were from 35 to 75% two-dimensional gametophytes (the remainder were filamentous), and on 100% they were all filamentous. Also, the higher the concentration, the greater the degree of branching. At least 40% of those filamentous gametophytes on 75% liquid endosperm had produced two-dimensional gametophytes at the end of some of the filaments (*Fig. 3*). Thus coconut milk from young- and medium-aged coconuts possesses a factor which will suppress the development of the terminal cell. The factor can be inactivated, presumably by metabolism, because when in low enough concentrations the filaments can revert and form two-dimensional gametophytes. Thus it should be possible to produce clones of even-aged gametophytes by suitable manipulation of the medium using coconut milk.

Low concentrations of liquid endosperm from young- and medium-aged coconuts increased the rate of growth of the gametophytes. Therefore coconut milk may be a useful medium supplement to accelerate the production of sporophytes in those species in which the gametophyte matures slowly.

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Studies in Lycopodiaceae, I. Observations on the Structure of the Sporangium Wall

BENJAMIN ØLLGAARD*,[1]

In this century several attempts have been made to classify the species of Lycopodiaceae *sensu lato* into natural groups. The most important ones are Rothmaler (1944), Herter (1949–50), and Wilce (1972). Owing to different approaches to the problem, their conclusions have differed considerably.

Herter's classification was published in several minor papers during the first half of the century and was adopted by Nessel (1939), but it was not published in full until 1950. It was based on worldwide herbarium studies. Herter recognized two genera, *Urostachys* and *Lycopodium*. The former comprised species with regularly forked (isotomous) stems, known as the *L. selago* and *L. phlegmaria* groups. *Lycopodium* contained all the unequally forked (pseudomonopodial) species. These genera were subdivided into subgenera, sections, and series.

Rothmaler based his classification mainly on gametophyte morphology. His genus *Huperzia* is identical with Herter's *Urostachys*, but the name was changed for nomenclatural reasons. Rothmaler split Herter's genus *Lycopodium* into three genera: *Lycopodium* (the *L. clavatum* group), *Diphasium* (the *L. complanatum* and *L. scariosum* groups), and *Lepidotis* (the *L. inundatum*, *L. cernuum*, and *L. laterale* groups). With regard to the species contained in the genera, Rothmaler largely adopted the subgenera or series of Herter. This classification has been adopted in several new Floras.

The study by Wilce (1972) provides evidence from spores. On the basis of both spore and sporophyte characters, she recognizes three major groups. In contrast to Rothmaler, she does not find these sufficiently distinct to give them rank of genera, but prefers the status of subgenera of one genus, *Lycopodium*. She unites the *L. clavatum* and *L. complanatum* groups into subg. *Lycopodium* and places here *L. casuarinoides*, *L. volubile*, and *L. deuterodensum*, which Rothmaler placed in *Lepidotis* and Herter placed in the *L. cernuum* group. According to Wilce, there are three subgenera: *Urostachys* Pritzel (=*Huperzia* Bernh.), *Lepidotis* (Pal. Beauv.) Baker (=*Lycopodiella* Holub emend. Pic. Ser.), and *Lycopodium* (including *Diphasium* Presl and the three species mentioned above).

It is the aim of the present study to revise the supra-specific taxonomy of the Lycopodiaceae in the light of evidence from the general sporangium wall structure. A large number of species representing the most important species groups was studied. They fall into three groups that coincide with the subgenera proposed by Wilce (1972). The characters appear to be very distinct and to form a valuable supplement to the apparently few clearcut characters in this family. They may, therefore, help to define the taxa within the family, and, indeed, have shed light on the affinity of a few species of uncertain position. Since the results of the

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present study support the ideas of Wilce, her classification of *Lycopodium* has been adopted in this paper. In addition to *Lycopodium,* the monotypic genus *Phylloglossum* is also treated.

Literature dealing with variation in the sporangium wall structure is scarce. Englert (1925), in a study of the anatomy of mainly South American species, described the major variation in sporangium wall structure, but he overlooked some details and reached conclusions different from those presented here. Wilce (1965) compared the structure in species of *Lycopodium* sect. *Complanata* (subg. *Lycopodium)* with *L. annotinum, clavatum, lucidulum, obscurum,* and *phyllanthum,* but not with species of subg. *Lepidotis*. Rolleri de Dougherty (1972), dealing with the anatomy of some Argentinean species, did not include observations of subg. *Lepidotis*.

MATERIALS AND METHODS

The materials for the present study were herbarium specimens and plants preserved in FAA representing *Phylloglossum* and about 80 species of *Lycopodium s. l.* About 40 of the latter belong to subg. *Urostachys*. This is about 10% of the total number of species placed in the group by Herter (1950). Fifteen species (ca. 50%) of subg. *Lepidotis* and 25 species (ca. 40%) of subg. *Lycopodium* were studied. Especially in the case of subg. *Urostachys* the species representation may seem small, but nearly all of Herter's species groups are included.

The number of specimens examined per species varies from 1 to 18; since intraspecific variation is negligible for the character studied, several species were checked by single specimens only.

Material was taken from specimens in the following herbaria: Herbarium Jutlandicum (AAU), Botanical Museum, Copenhagen (C), Field Museum (F), Botaniska Institutionen, Göteborgs Universitet (GB), Gray Herbarium (GH), Kew (K), München (M), and U. S. National Herbarium (US). I wish to express my gratitude to the curators of these institutions for permission to study the specimens in their care. Material preserved in FAA was collected by the author during an expedition to Ecuador in 1973 (35 species) and in Denmark.

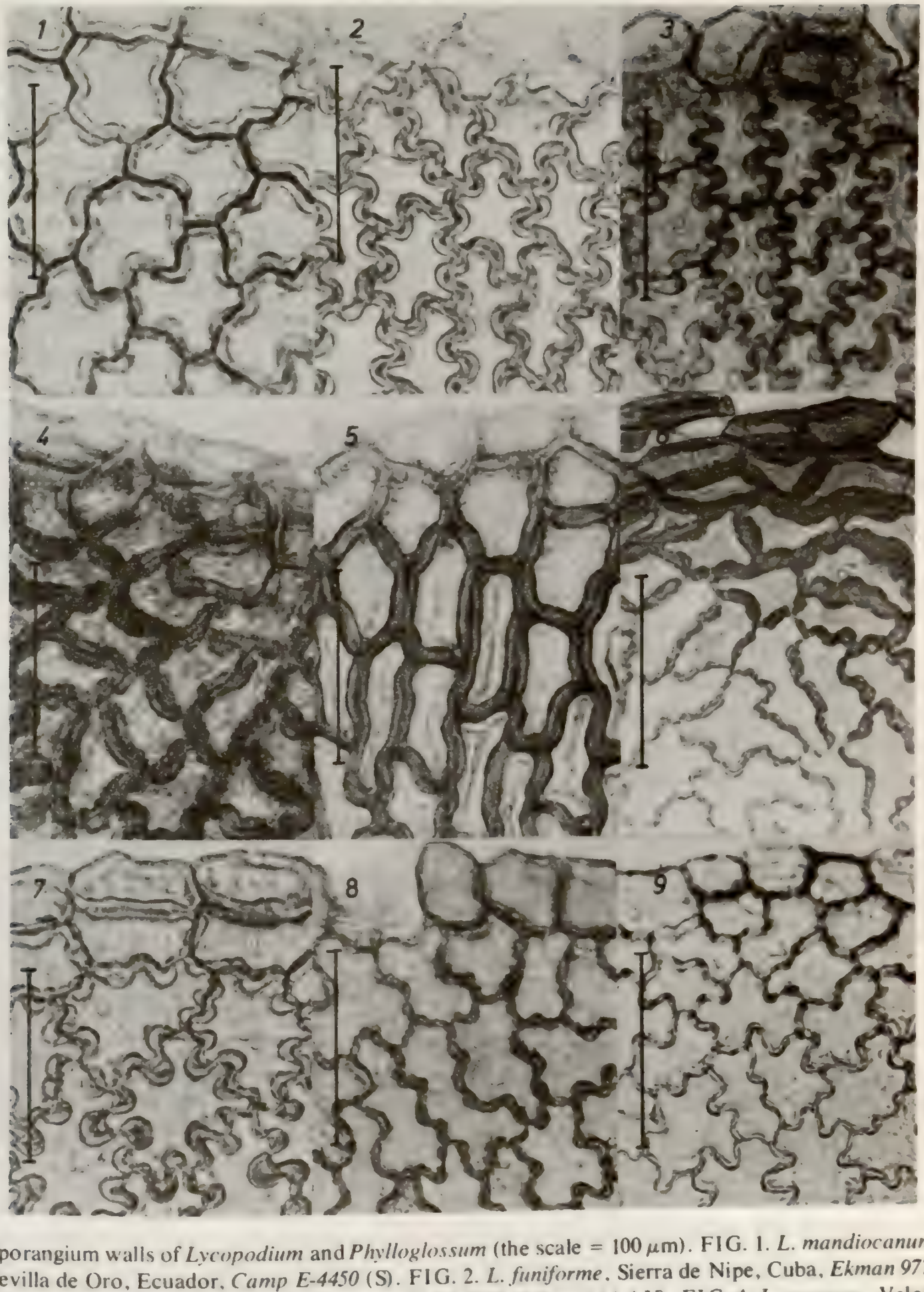
The method of observation is simple and even convenient enough so that the character of the sporangium wall can be used in keys. A small portion of a strobilus with mature sporangia is softened with a drop of alcohol to allow removal of a sporangium without damaging the adjacent sporophylls. The sporangial valves are separated and heated in a drop of phloroglucinol–HCl, and then the walls of the outer surface examined under the microscope.

For the sake of uniformity, the photographs (*Figs. 1–25*) were taken from a region near the stomium on or near the median line of the sporangium. Magnification is indicated by a 100 μm scale on each figure.

In order to elucidate the nature of the thickenings, paraffin sections stained with safranin and fast green were prepared of representative species fixed in FAA or, in a few cases, of herbarium material softened in alcohol.

RESULTS

Sporangia in the Lycopodiaceae are reniform to subspherical. They open by a



Sporangium walls of *Lycopodium* and *Phylloglossum* (the scale = 100 μm). FIG. 1. *L. mandiocanum*, Sevilla de Oro, Ecuador, *Camp E-4450* (S). FIG. 2. *L. funiforme*, Sierra de Nipe, Cuba, *Ekman 9770* (S). FIG. 3. *L. selago*, Akershus, Norway, 19 Jul 1932, *Störmer* (AAU). FIG. 4. *L. crassum*, Volcán Sincholahua, Ecuador, *Holm-Nielsen et al. 6591* (AAU). FIG. 5. *L. phlegmaria*, Madagascar et Mauritius, Ex herb. Welwitsch (AAU). FIG. 6. *L. casuarinoides*, Kweichow, China, *Tsiang 4365* (S). FIG. 7. *P. drummondii*, Auckland, New Zealand, *Carse* (AAU). FIG. 8. *L. thyoides*, Nudo de Cajanuma, Loja, Ecuador, *Sparre 16554* (S). FIG. 9. *L. fastigiatum*, Mt. Egmont, New Zealand, *Lee 1963* (AAU).

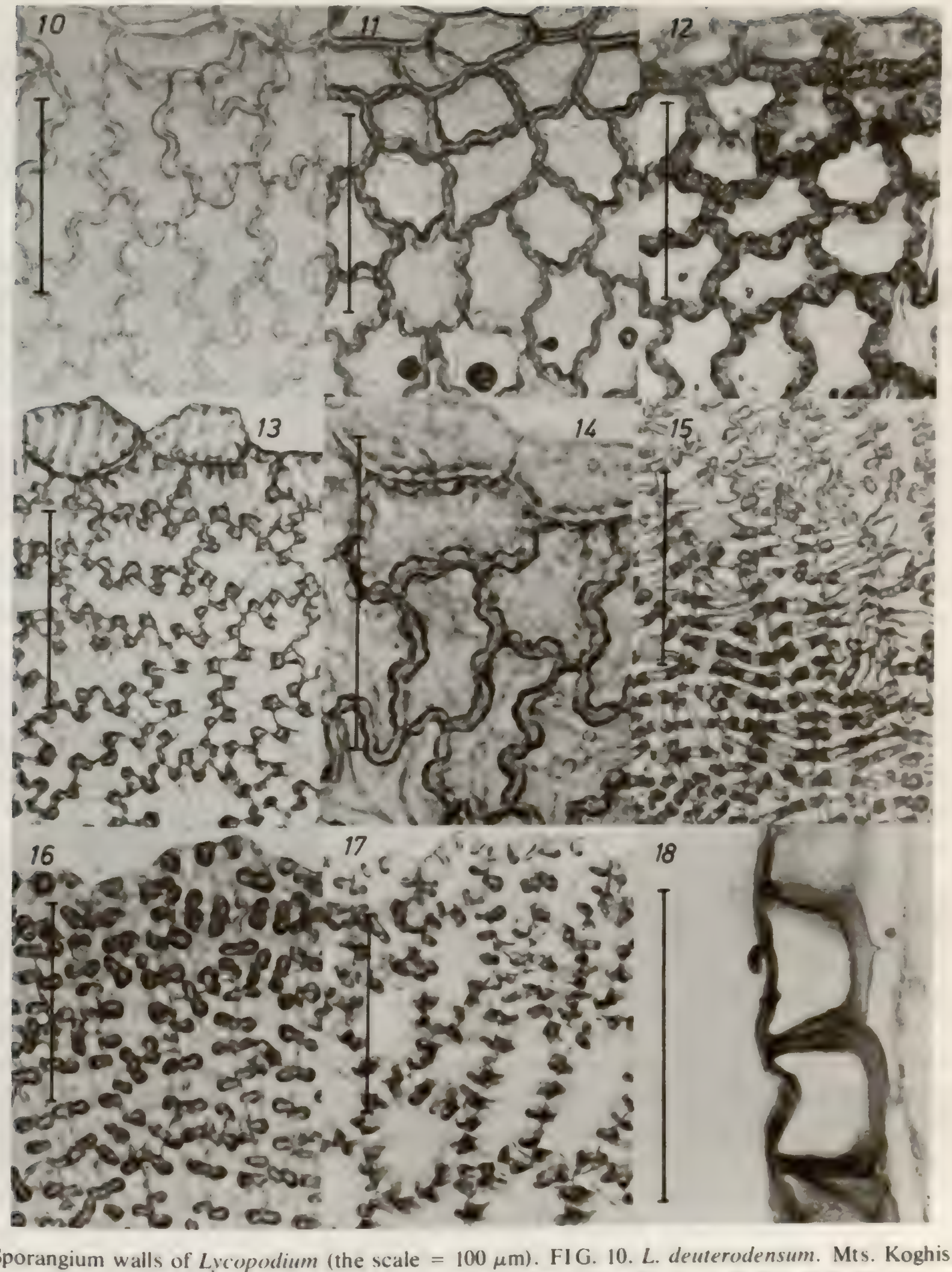
transverse slit which divides the sporangium into two valves at maturity. This occurs along a usually double row of transversely elongate, partly thin-walled stomium cells. In some species the valves are nearly equal (isovalvate), but in others the stomium is formed on the abaxial side of the sporangium, producing a large adaxial and a small abaxial valve (anisovalvate). The sporangium wall consists of two to several cell layers, of which the external one is characteristically developed and displays the variation which is the subject of this paper. With the exception of the stomium, the sporangial cells are generally elongate radially from the sporangium stalk. The cell shape varies gradually from narrow, elongate, and relatively thin-walled at the stalk, to isodiametric and with thicker walls near the stomium. The following descriptions apply to portions near the stomium where the characters studied are most clearly developed.

The structure of the outer cell layer is very uniform within a single species, but throughout the family a considerable range of variation is found. The term "side wall" means the anticlinal cell walls separating individual cells of the outer cell layer of the sporangium, whereas "inner wall" and "outer wall" refer to periclinal walls toward the interior and exterior of the sporangium, respectively. Three groups can be recognized on the basis of the distribution of thickenings and shape of the cell walls.

Subgenus Urostachys.—This group is characterized by sinuate side walls and thickened and lignified side and inner walls (*Figs. 1–5*). Variation within this group is in wall thickness and sinus shape. The wall thickenings are best studied in sections of sporangia. Here the side walls commonly increase in thickness toward the inner wall, which has the same thickness as the inner end of the side walls. In sections the thickenings appear U-shaped (*Fig. 18*). The side walls are smooth. When unsectioned whole mounts are examined, it is difficult to measure the exact thickness of the cell wall because it changes with the depth of focus. Generally it measures 5–10 μm. With the exception of *L. casuarinoides* and *Phylloglossum*, the general structure described above was found only in subg. *Urostachys*.

There is a certain variation in wall thickness and sinuosity which cannot be described in detail here, but a few examples are worth mentioning. For instance, in some high andean species (*L. rufescens*, the *L. crassum* group, *L. trencilla*, etc.) the cell walls are extremely thick (*Figs. 4* and *19*) and the sporangium valves more or less opaque. In contrast to this, some species (mostly from sheltered habitats) have comparatively thin-walled sporangia. Wilce (1965, pl. 31, f. 19) shows *L. lucidulum* to be as thin-walled as members of sect. *Complanata*. This was not confirmed by my specimens from eastern North America, which had all the sporangium cell walls about 7 μm thick.

The variation in sinuosity is gradual. In most species the sinuses are open and evenly rounded, but in the extremely thick-walled andean species mentioned above (*Fig. 4*) and in *L. phlegmaria* (*Fig. 5*) the sinuses are very shallow, even near the stomium. In *L. selago* (*Fig. 3*) the sinuses of the outer wall are far more deeply sinuate than those of the inner wall. Similar sinuosity was found in *Phylloglossum* (Fig. 7).



Sporangium walls of *Lycopodium* (the scale = 100 μm). FIG. 10. *L. deuterodensum*. Mts. Koghis, New Caledonia, *Franc 28* (S). FIG. 11. *L. volubile*, Nelson, New Zealand, 25 Feb 1949, *Skottsberg* (S). FIG. 12. *L. jussiaei*, Páramo del Castillo, Ecuador, *Camp E-1638A* (S). FIG. 13. *L. clavatum*, Valley of the Río Zamora, Ecuador, *Camp E-61* (S). FIG. 14. *L. alpinum*, Ustefjell, Norway, 7 Aug 1949, *Thuesen* (AAU). FIG. 15. *L. inundatum*, Gjerrild Nordstrand, Denmark, 26 Sept 1972, *Øllgaard* (AAU). FIG. 16. *L. cernuum*, Mera, Ecuador, *Mexia 6965* (US). FIG. 17. *L. carolinianum*, Quebrada de Corinto, Colombia, *André 2735* (NY). FIG. 18. Section of *L. capellae*, Páramo del Angel, Ecuador, *Holm-Nielsen et al. 5467* (AAU).

Subgenus Lycopodium.—In this group the side walls are lignified and sinuate, but not notably thickened. The wall thickness is 3–5 μm. I have found only species of subg. *Lycopodium* to have this structure.

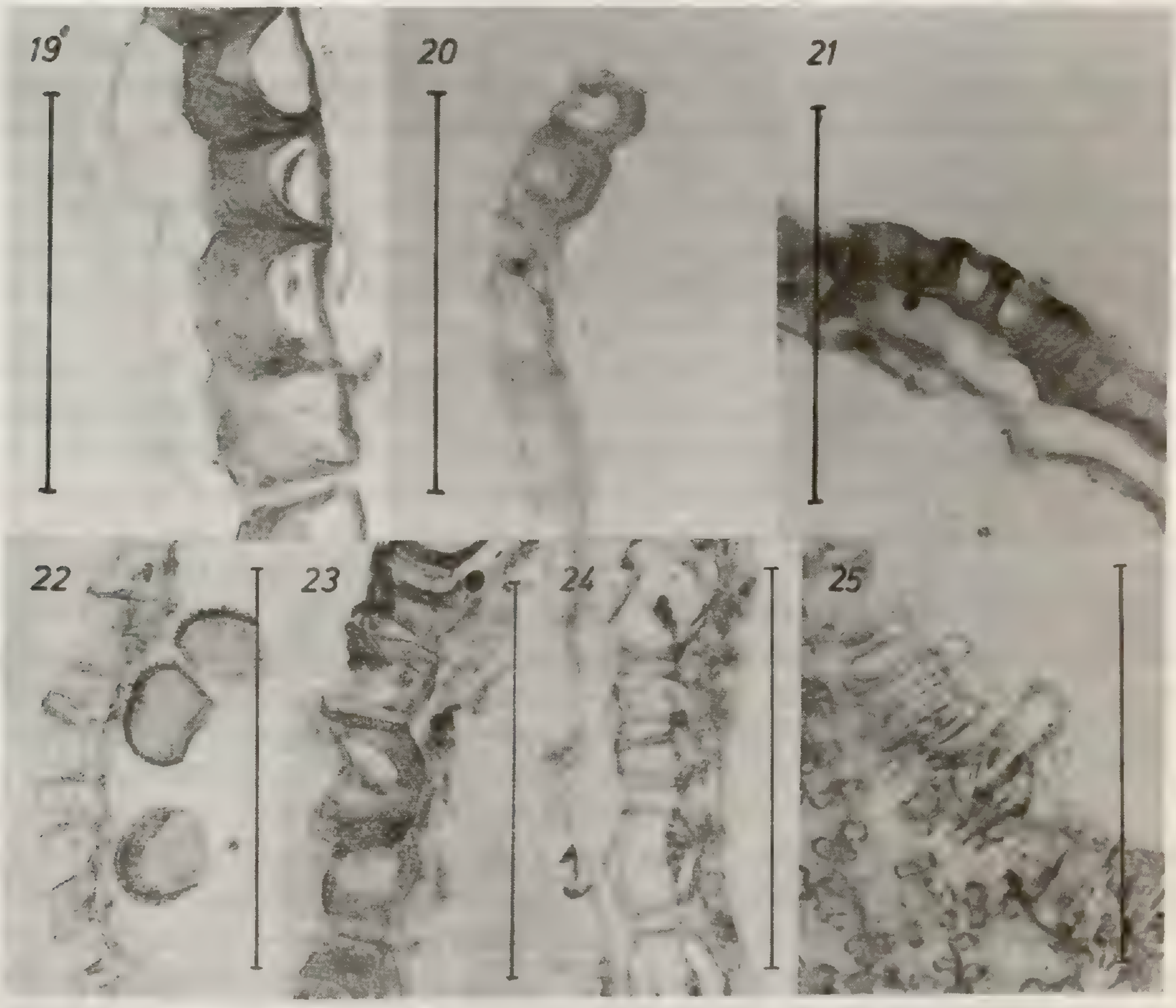
The side wall sinuses in this group are open and evenly rounded (*Figs. 8–11*) in the majority of species (sect. *Complanata, L. confertum, deuterodensum, fastigatum, magellanicum, obscurum, paniculatum, spurium,* and *volubile*). In the *L. scariosum* group, which includes *L. decurrens, gayanum, jussiaei,* and *scariosum,* the sinuses have the same shape, but the side walls are finely curled (*Fig. 12*). In *L. annotinum* the side walls in some sinuses apparently end in small, nodular thickenings. This is carried to an extreme in the *L. clavatum* group, which includes *L. clavatum, contiguum, venustulum,* and *vestitum,* where almost all sinuses end in a similar structure (*Fig. 13*). As indicated by Wilce (1965, p. 81), this very characteristic appearance is not due to thickenings as described by Englert. Careful examination at high magnification and study of sections reveal them to be narrow sinuses of the cell wall, accommodating themselves to dissimilar shapes of the inner and outer walls. Therefore, this structure can hardly be regarded as distinct from the open, evenly rounded type. In *L. alpinum (Fig. 14), annotinum, complanatum, obscurum,* and *thyoides* the surfaces of the side walls are not smooth, as they are in most species in this group, but are instead densely and irregularly pitted, resembling those of *L. casuarinoides,* although less thickened. In *L. casuarinoides* the side walls are conspicuously thickened, as are the inner walls of the multiseriate stomium cells (*Figs. 6* and *20*). Nearly all cells of the abaxial valve are heavily thickened and lignified. In some portions of the adaxial sporangium wall the side walls are irregularly thickened or pitted, and sometimes appear like strings of pearls, a feature never seen in subg. *Urostachys*. On the large adaxial valve several nonfunctional stomata were observed.

Subgenus Lepidotis.—This group has straight, thin, and unlignified side walls, with the exception of several semiannular or nodular lignified thickenings in each cell. This structure has been found throughout and exclusively in subg. *Lepidotis*. The cells of this group thus are strikingly different from those of the other two groups.

The semiannular thickenings are parallel half-rings which open towards the outer cell wall (*Figs. 15* and *23*). Often the half-rings fork or the portions on the inner wall from a few half-rings may be confluent, forming an irregular, thickened plate on the inner wall. Well developed semiannular thickenings predominate in the *L. indundatum* group, which includes *L. adpressum, alopecuroides,* and *inundatum*. The nodular type (*Figs. 16* and *24*) is probably derived from the semiannular type, simply by reduction of the portion on the inner wall. Nodular thickenings were overlooked by Englert, who described all thickenings in this group as semiannular. There are several indications of this process in intermediate types, ranging from the mere lack of lignification of the portion on the inner wall to scarcely visible ridges connecting pairs of nodular thickenings. The nodular type is predominant in the *L. cernuum* group, which includes *L. cernuum, lehmannii, pendulinum,* and *trianae*. Various intermediate types are found in *L. contextum* and *laterale* and in the *L. carolinianum* group, as in *L. carolinianum (Fig. 17)*.

DISCUSSION

The preceding findings make it possible to distinguish three main groups within *Lycopodium*. The nonsinuate group with semiannular or nodular thickenings is very distinct from both of the sinuate groups. Considering both spore and sporophyte characters, such as branching pattern (Øllgaard, in prep.) and



Sections of sporangium walls of *Lycopodium* and *Phylloglossum* (the scale = 100 μm). FIG. 19. *L. crassum*, Páramo del Angel, Ecuador, *Holm-Nielsen et al. 5464* (AAU). FIG. 20. *L. casuarinoides*, Kweichow, China, *Tsiang 4365* (S). FIG. 21. *P. drummondii*, Auckland, New Zealand, *Carse* (AAU). FIG. 22. *L. deuterodensum*, Mts. Koghis, New Caledonia, *Franc 28* (S). FIG. 23. *L. alopecuroides*, Valle de Zamora, Ecuador, *Holm-Nielsen et al. 4099* (AAU). FIG. 24. *L. pendulinum*, Valle de Zamora, Ecuador, *Holm-Nielsen et al. 3736* (AAU). FIG. 25. *L. latèrale*, whole mount showing thickenings in side view, Sydney, Australia, *Nash 200* (S).

strobilus construction, in combination with the uniform sporangium wall structures described here, there is hardly any doubt that Wilce's subg. *Lepidotis* is very natural, although its members are diverse in habit. Its division into two genera, *Lycopodiella* and *Palhinhaea*, proposed by Holub (1964) and by Vasconcellos and Franco (1967) finds no support in my material. The two sinuate groups are less sharply distinct, although this does not reflect any difficulty in distinguishing them by characters other than those of the sporangium wall. The change from thin to

thick walls or vice-versa is likely to be a simple genetic process, and so the thick walls found in *L. casuarinoides* can be interpreted as a convergent development, rather than as an indication of relationship to subg. *Urostachys*.

At present the knowledge of sporangium structure variation in subg. *Urostachys* is too incomplete to suggest taxonomic relationships within this group, but in a revision of this subgenus a closer study of these characters might be rewarding, even though the variation is subtle.

In subg. *Lycopodium*, the sporangium wall characters seem to correlate with the species groups. Thus, the *L. clavatum* group is characterized by pseudonodular sinuses. Whether or not the scattered pseudonodules in *L. annotinum* indicate a close relationship to *L. clavatum* is uncertain. I tend to think that they do not, because the walls of *L. annotinum* are irregularly pitted and not smooth as in *L. clavatum*. This is also the case in *L. obscurum*, which has no pseudonodules. Because of other similarities, the affinity of *L. annotinum* perhaps is with *L. obscurum*.

The *L. scariosum* group is characterized by finely curled side walls, which separates it from the *L. complanatum* group and accentuates the heterogeneity also found, for instance, in leaf morphology in *Diphasium sensu* Rothmaler. As pointed out by Wilce (1972), the generic name *Diphasium* includes the *L. scariosum* group, but not the *L. complanatum* group. If the divergence which caused Rothmaler to separate the *L. clavatum* group from the *L. complanatum* group on the generic level is accepted, then also the *L. scariosum* group should be separated from the *L. complanatum* group generically. This would lead to recognizing at least seven genera within the present subg. *Lycopodium*. It certainly would be very difficult for non-specialists to perceive such genera.

The monotypic genus *Phylloglossum* was not treated by Wilce. Harris (1955, p. 57) and Breckon and Falk (1974) agree that the affinity of the spore characters is with subg. *Urostachys*, especially with sect. *Phlegmaria*. This is confirmed, at least for the subgenus, by sporangium wall characters, which resemble those of *L. selago* closely. Rothmaler, however, considered *Phyloglossum* to be a close relative of *L. cernuum*. Because of the similarity of its gametophyte and sporophyte to the gametophyte and protocorm stage of *L. cernuum*, it has often been supposed to be a permanently embryonic form of this species. The results of Freeberg (1957, 1962) and Freeberg and Wetmore (1957) indicate that gametophyte and protocorm structures are ecologically influenced and do not necessarily indicate taxonomic affinities. Evidence from the sporangium wall clearly disproves Rothmaler's idea.

Sporangium structure may give a clue to the affinity of species of uncertain position. For instance, *L. sprucei* was regarded as an intermediate between the *L. clavatum* and *L. inundatum* groups (Baker, 1887, p. 24) or between *L. contiguum* and *L. cernuum* (Nessel, 1939, p. 313[2]). However, Baker, Nessel, Rothmaler (1944) and Herter (1950, p. 94) all referred this species to the *L. clavatum* and *L. annotinum* groups, presumably because of its distinct sporophylls. Its nonsinuate

[2]Nessel's figure 72 actually is *L. contiguum* (subg. *Lycopodium*), not *L. sprucei*.

sporangium cell walls with semiannular thickenings, rugulate spores (Øllgaard, unpubl.), and acicular, terete leaves demonstrate its affinity to subg. *Lepidotis*. A comparison with the type of *L. contextum*, which was referred to the *L. inundatum* group of subg. *Lepidotis* by the same authors, proved that *L. contextum* (the earlier name) is identical to *L. sprucei*.

Rothmaler (1944) included *L. deuterodensum* and the scandent species *L. casuarinoides* and *L. volubile* in the genus *Lepidotis*. This was in accord with Herter in Nessel (1939, Hauptgruppe *Cernuostachys*) and Herter (1949–50, sect. *Cernuistachys*). Since gametophyte characters were regarded as important by Rothmaler, this arrangement is puzzling, for it was known that the gametophytes of *L. volubile* are subterranean and holosaphytic and that its sporelings develop a large foot and protocorm (Holloway, 1915; Chamberlain, 1917). In *L. deuterodensum* sporelings have been found with a large foot ca. 4 cm below the ground surface (Holloway, 1909, p. 360). These characters point to an affinity with *Lycopodium* or *Diphasium* in Rothmaler's sense, rather than to *Lepidotis*. The sinuate and lignified cell walls and the spore pattern found by Wilce (1972) confirm their lack of affinity with *Lepidotis*.

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SHORTER NOTES

NOTES ON SOME OPHIOGLOSSACEAE IN THE GEORGIA COASTAL PLAIN.—Prior to Norsworthy's list of ferns of Echols County (Amer. Fern J. 56: 55-57. 1964) the only record of *Ophioglossum* in the Georgia Coastal Plain was *O. nudicaule* from Effingham County (McVaugh, R. & J. H. Pyron. 1951. Ferns of Georgia, p. 128). *Ophioglossum crotalophoroides, O. petiolatum,* and *Botrychium lunarioides* have not been reported from the Coastal Plain. Our collections reveal that all four ferns occur within the area and that their supposed rarity is most often a lack of discriminating collecting.

Ophioglossum crotalophoroides Walter, the Bulbous Adder's-tongue, reaches its peak of development in the late winter months and is common in open, disturbed habitats such as lawns, roadsides, and clearings for utility lines. We have specimens from the following 26 counties: Appling, Atkinson, Ben Hill, Berrien, Brooks, Calhoun, Charlton, Clinch, Coffee, Colquitt, Cook, Daugherty, Decatur, Echols, Grady, Irwin, Jeff Davis, Lanier, Lowndes, Mitchell, Telfair, Thomas, Tift, Turner, Wilcox, and Worth.

Ophioglossum nudicaule var. *tenerum* Clausen, the Least Adder's-tongue, seems to prefer moist habitats of sandy and peaty soils. Our collections include specimens from 5 counties: Atkinson, Coffee, Echols, Lanier, and Tift.

Ophioglossum petiolatum Hooker, the Stalked Adder's-tongue, forms large clones by producing adventitious buds on its roots, and frequently is found in moist, alluvial soils of semi-shaded habitats. Areas beneath highway bridges have proven to be ideal collecting sites. We have specimens from 18 counties: Atkinson, Berrien, Charlton, Chatham, Clinch, Coffee, Echols, Effingham, Grady, Irwin, Jeff Davis, Lanier, Long, Lowndes, Pierce, Telfair, Thomas, and Ware.

Botrychium lunarioides Swartz, the Prostrate Grape Fern, was discovered during a search for the Bulbous Adder's-tongue on a grassy, clay-loam roadfill in Cook County on March 17, 1972 (*Norsworthy & Carmer 152*). The fertile segments of the stalks alone led to its discovery, for its leaves were camouflaged by the grass and were not discernible until a plant was uprooted with a trowel. In February, 1973, a colony was discovered growing in sandy soil of a churchyard in Echols County (*Norsworthy 252*). Some plants were growing beneath a small Red Cedar tree, but the majority were growing in an open exposed area with a scanty grass cover. The colony reappeared in 1974 and appears to be well established, despite foot traffic in the area.

Our work corroborates the findings of Thomas (Amer. Fern J. **61**: 39-41. 1971; **63**: 166. 1973) in Louisiana and Mississippi. Our efforts have been more concentrated on the Bulbous Adder's-tongue. However, we are convinced that continued meticulous collecting will prove that all these species are more widespread than the above records indicate.

Specimens of our collections are on deposit in the Valdosta State College Herbarium.—*Wayne R. Faircloth and Mary Norsworthy, Dept. of Biology, Valdosta State College, Valdosta, GA 31601.*

DRYOPTERIS NEO-WHERRYI RECORDED FOR WEST VIRGINIA.—On June 8, 1974 and again on July 18 while in the company of Ronald Fortney, I collected a species of fern that I was unable to identify. The plants were growing in a moist, shady ravine about 11 miles south of Morgantown, Monongalia County, West Virginia, on Huntington silt loam (pH 5), which is derived from Buffalo sandstone. Dr. Warren H. Wagner, Jr., of the Department of Botany, University of Michigan, identified the specimens as *Dryopteris neo-wherryi*, which is the hybrid between *D. goldiana* and *D. marginalis*. Voucher specimens, *Breiding 825a, b, 826a, b, c,* have been deposited in the West Virginia University herbarium (WVA) at Morgantown. As far as is known, this is the first record for West Virginia. Wagner (Castanea 31:136. 1966) reports it from Michigan to New England and south to southwestern Virginia.—*Michael A. Breiding, 38 Edgehill Street, Morgantown, WV 26505.*

SOME LYCOPODIUMS NEW TO WESTERN KENTUCKY.—The Jackson Purchase, a geologically unique, eight-county region in the extreme western tip of Kentucky, has been studied by Kentucky botanists only spasmodically. It represents the northern extension of the Mississippi Embayment Province, a lowland with little relief which was covered by the Gulf of Mexico during the Cretaceous and Tertiary. The region is typified by soils rich in sands, gravels, and clays. Extensive field study throughout the Purchase during the past three years has established many new records and range extensions. Field study travel was supported by Institutional Research Grant #162 from Murray State University.

Lycopodium flabelliforme (Fern.) Blanch., the Ground Cedar or Running Pine, is common throughout the southeastern United States in dry to moist fields, dry upland woods, and in the mountains. In the "Vascular Plants of Illinois," Jones and Fuller record it for southern Illinois, but no records for far-western Kentucky could be established. On 11 May 1971 we discovered a single colony in a honeysuckle thicket in second-growth woods in Marshall County (*Johnson 4292*).

Lycopodium prostratum Harper, the Foxtail Club-moss, and *L. appressum* (Chapm.) Lloyd & Underw., the Southern Bog Club-moss, are found chiefly throughout the outer Coastal Plain of the southeastern United States in acid bogs, sandy swales or fields, and pinelands. Both are extremely rare inland, but we discovered both in Calloway County in a swampy seepage area which also supports a large moss population. *Lycopodium prostratum* (1 Sept 1971, *Johnson 4576*; 12 Sept 1973, *Johnson & McCoy 1001*; 6 Oct 1973, *McCoy 2311*) occupies the wetter sites of the depression. *Lycopodium appressum* (12 Sept 1973, *Johnson & McCoy 1012*; 6 Oct 1973, *McCoy 2315*) occurs around the margins of the depression on generally drier sites. The discovery of these plants is a significant northwestern range extension for both.

Specimens of the collections cited are on deposit in the herbarium of Murray State University (MUR).—*Robert G. Johnson, Dept. of Biology, Murray State University, Murray, KY 42071* and *Thomas N. McCoy, 904 Vine St., Murray, KY 42071.*

NEW COMBINATIONS IN AMERICAN BOLBITIS SPECIES.—From my studies on the American species of the genus *Bolbitis*, I have found it necessary to make some new combinations. For practical reasons these are published here, prior to an extensive account of all the species that will include full synonymies. The heterotypic synonyms listed below refer to names now in general use. The types cited all have been studied. The herbarium abbreviations are those proposed by Lanjouw and Stafleu in the fifth edition of the "Index Herbariorum" (1964).

Bolbitis hastata (Fourn.) Hennipman, comb. nov.

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E. Hennipman, Rijksherbarium, Schelpenkade 6, Leiden, Netherlands.

REVIEW

"CYTOGEOGRAPHIC STUDIES ON DRYOPTERIS OF JAPAN," by Haruki Hirabayashi. iv + 176 pp. 1974. Published by the Harashobo Co., Tokyo. 4000 yen; ca. $13.50.—No fern genus has attracted so much biosystematic attention in the past ten years as *Dryopteris*, a major component of the temperate pteridophyte flora of the world. Dr. Hirabayashi has been publishing on the cytology of this genus since 1966. He brings together here in a nicely organized and hardbound volume his and others' research on the cytogeography of Japanese *Dryopteris*, including some new records. The book is based upon a doctoral thesis he submitted to the Tokyo University of Education.

In Japan *Dryopteris* comprises well over twice as many taxa as are known in all of North America north of Mexico, approximately 90 vs. 40. Chromosomes have been observed in 77 of the Japanese species and hybrids. The results differ in various ways from the American situation. For example, apogamy is extremely common, with 36 apogameons (versus none in the United States and Canada). There is a lower incidence of hybrids, less than 25 per cent (in contrast to the more than 60 per cent reported in the temperate New World). Hirabayashi lists only two taxa that occur both in Japan and North America: *Dryopteris fragrans* and the fern he calls *D. austriaca*.

Hirabayashi documents the chromosomes of 22 sexual diploid taxa, 6 sexual tetraploids, 36 apogameons (30 of these triploid, 5 diploid, and 1 tetraploid), and 15 sterile hybrids (diploids, triploids, and tetraploids). Most of the cytological squashes shown in the photographs and ink tracings are clear, with a few exceptions (e.g., pl. 8, b; pl. 9, b; and pl. 10, a, c, d). In Table 6, only single counts for each hybrid taxon are cited. As I have found,[1] single counts without indication of variability can be misleading. In American *Dryopteris* some hybrid combinations have no pairing variability at all, but others have as few as five to as many as 41 pairs. Such differences have cytogenetic significance. Hirabayashi's interpretations of the chromosome units he observed as comprising only singles and pairs conform to what most workers are finding: multivalents are either exceedingly rare or absent.

Japan's mountainous, insular geography and south-north latitudinal span of some 1300 miles creates diverse environments for plants. Hirabayashi separates the species and hybrids of *Dryopteris* into several distribution types and correlates these ranges with their cytogenetic properties. From these correlations he concludes that "the distribution ranges of all triploid and tetraploid populations of Japanese *Dryopteris* are narrower than those of diploid ancestors," in contrast to a general belief that polyploids tend to have wider distributions than diploids.

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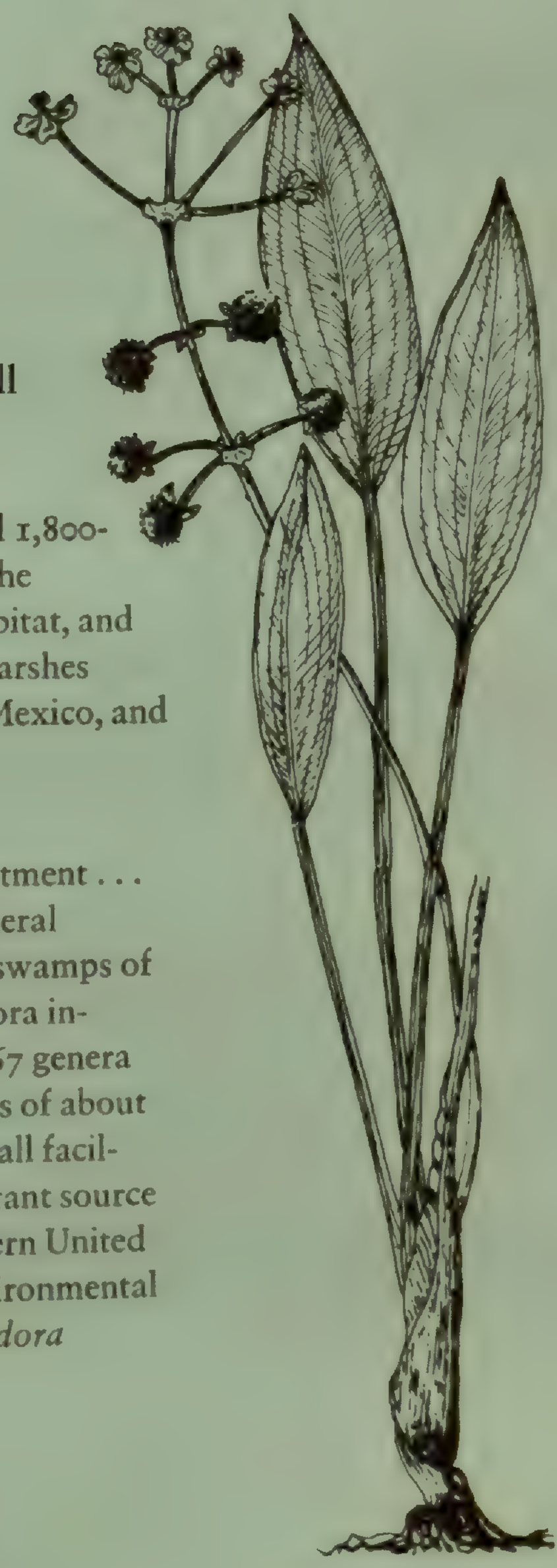

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The Spores and Taxonomy of Isoëtes butleri and I. melanopoda

W. CARL TAYLOR, ROBERT H. MOHLENBROCK, and JUDITH A. MURPHY*

Isoëtes L. is a genus of lycopods consisting of at least 60 species, and is of worldwide distribution. Members of this genus are small, herbaceous, perennials and are aquatic, amphibious, or terrestrial. *Isoëtes* is sometimes referred to by the common name of Quillwort, which refers to its elongate, quill-like leaves. Because its grass-like or rush-like habit often makes it difficult to discern from surrounding vegetation, it is often overlooked in the field.

Due to its rather peculiar morphology, *Isoëtes* has been the subject of some interesting statements. Linnaeus (1754, p. 486) described the staminate and pistillate flowers of *Isoëtes* as incomplete and solitary in the axils of the leaf bases. Engelmann (1878) stated, "The species of *Isoëtes* are the simplest vascular plants known."

The tufted, quill-like leaves of *Isoëtes* arise from a thick, flattened, corm-like, underground axis. A sporangium is located adaxially at the base of each fertile leaf; just above the sporangium is a small, flat, generally triangular ligule. The outer wall of the sporangium may be more or less covered by a flap of tissue called the velum. *Isoëtes* is heterosporous, producing megaspores or microspores in sporangia on separate leaves.

Monographers have used characters of the habitat, leaf, ligule, velum, and sporangium in the taxonomy of *Isoëtes*. In addition, the size and ornamentation of the megaspores have often been used to separate the various taxa more precisely.

The recognition of *Isoëtes melanopoda* Gay & Durieu and *I. butleri* Engelm. as distinct species has been questioned by a number of workers, from Pfeiffer in her monograph of the Isoëtaceae (1922) to Evans in "The Manual of the Vascular Flora of the Carolinas" (1968). Most recently, the validity of *I. butleri* as a species has been questioned by Kral (1973, p. 367), who stated that "leaf, ligule, velum, and corm characters all vary too much for accurate delimitation of the taxa." However, the spores of these two species normally do differ in size. The megaspores of *I. butleri* are usually greater than 480 μm in diameter, whereas those of *I. melanopoda* are usually less than 450 μm across. It should be noted, however, that intermediate spore sizes do exist in both species.

Since recently collected material from Arkansas and Illinois proved difficult to identify with certainty using the traditional morphological characters, the authors decided to examine both megaspores and microspores of these two taxa under the scanning electron microscope (SEM). Spores for examination were chosen from authentic or type material located in the Missouri Botanical Garden (MO) and from Arkansas, Illinois, and Missouri collections which, by the standards of previous monographers, fit either *I. melanopoda* or *I. butleri*. The spores were prepared for examination by mounting them on double-sided plastic tape and

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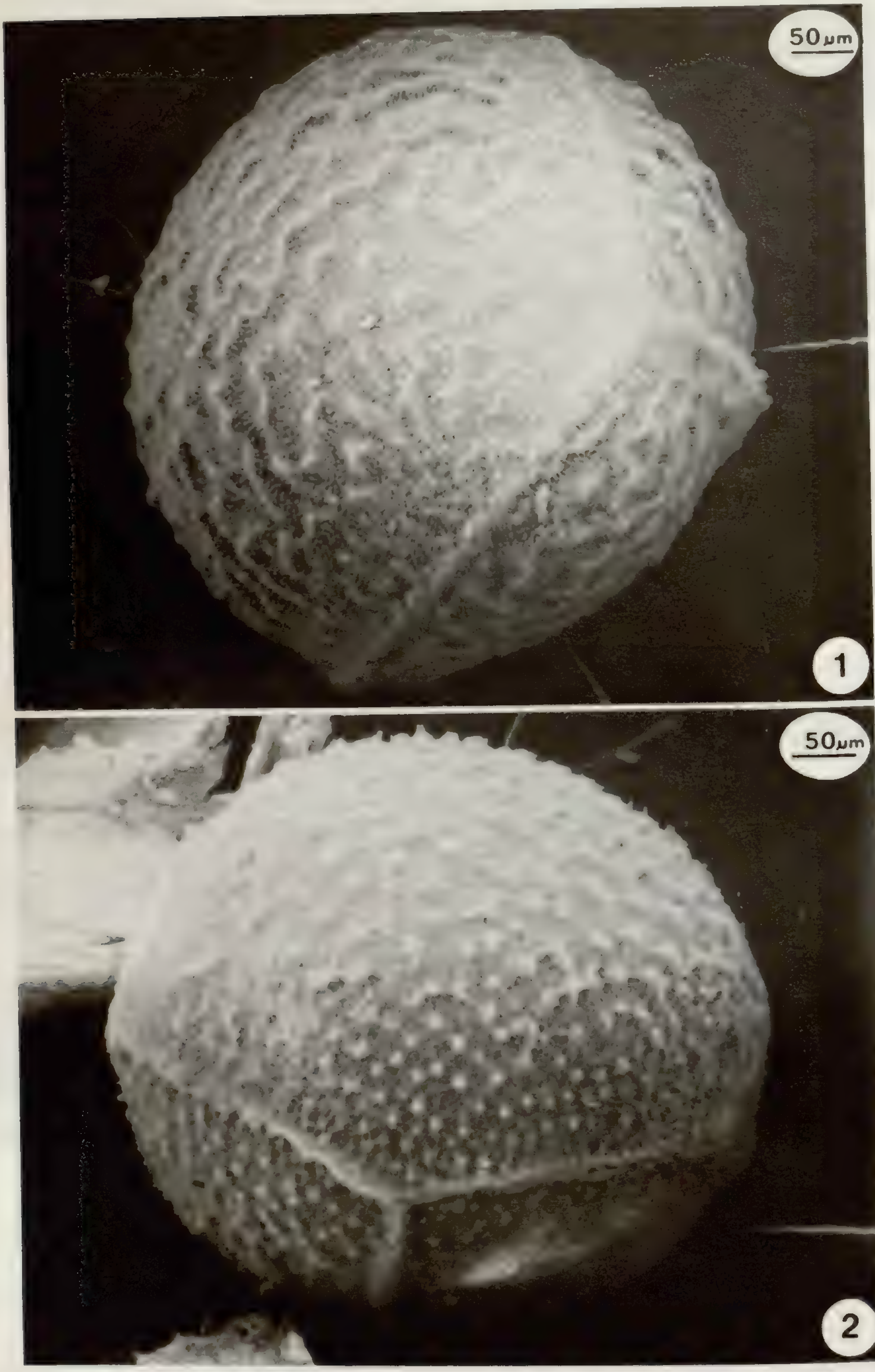
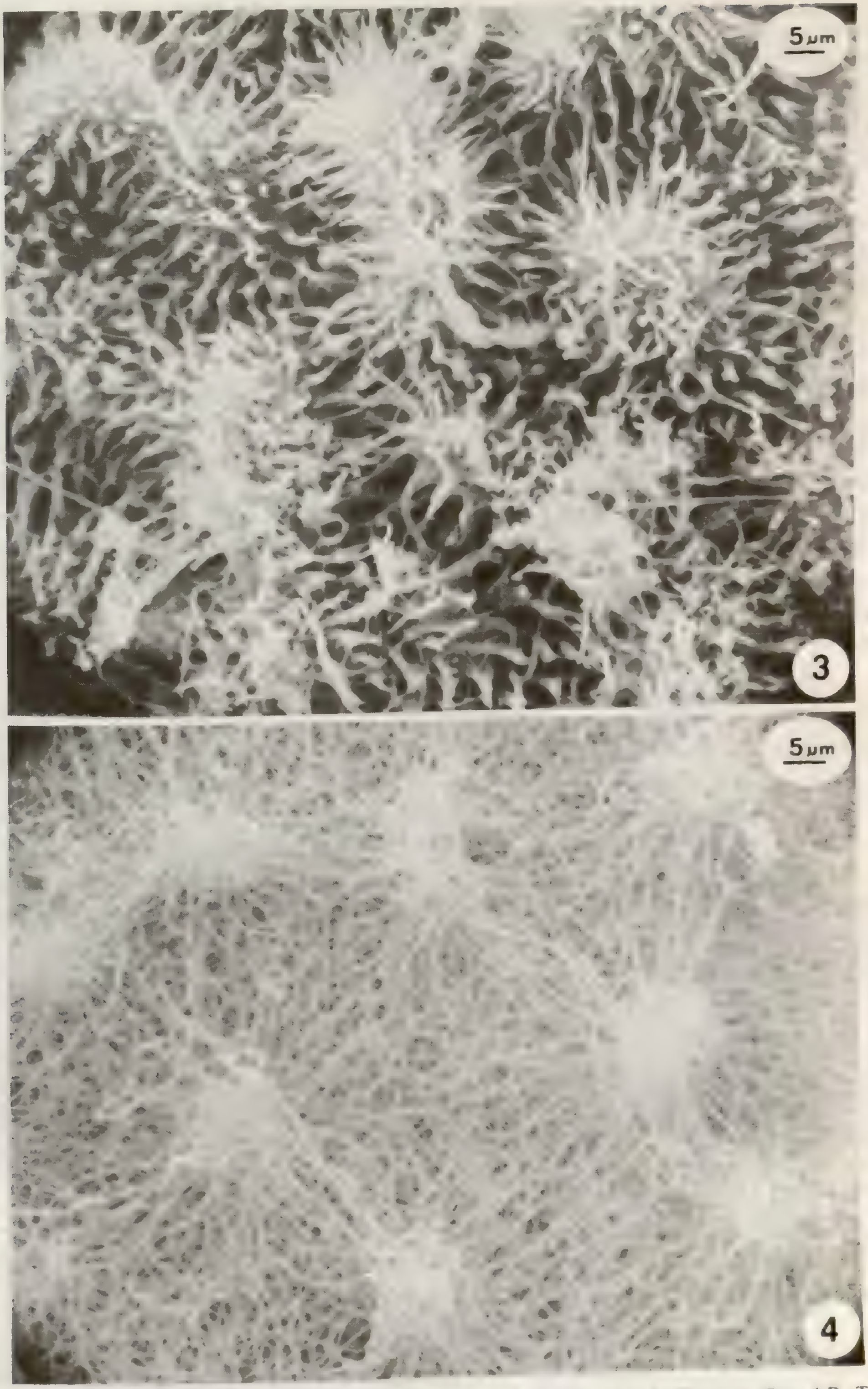


Isoëtes megaspores. FIG. 1. *I. melanopoda*, Petit Jean State Park, Conway Co., AR. *Taylor 957* (SIU). FIG. 2. *I. butleri*, Limestone glade, Newton Co., AR, *Taylor 1228* (SIU).



Isoëtes megaspore surfaces. FIG. 3. *I. melanopoda*, Petit Jean State Park, Conway Co., AR, *Taylor 957* (SIU). FIG. 4. *I. butleri*, Limestone glade, Newton Co., AR, *Taylor 1288* (SIU).

coating them first with a thin layer of carbon followed by two layers of palladium gold, one at a high angle and one at a low angle. A Cambridge Mark II-A SEM was used.

Our observations indicate that both the megaspores and the microspores of *I. melanopoda* and *I. butleri* are markedly and consistently different. We have found this to be true at various stages of maturity, despite Pfeiffer's (1922, p. 152) comment that the two might be developmental stages or ecotypes of the same species. Differences in spore ornamentation can be seen under the SEM which have not been described previously.

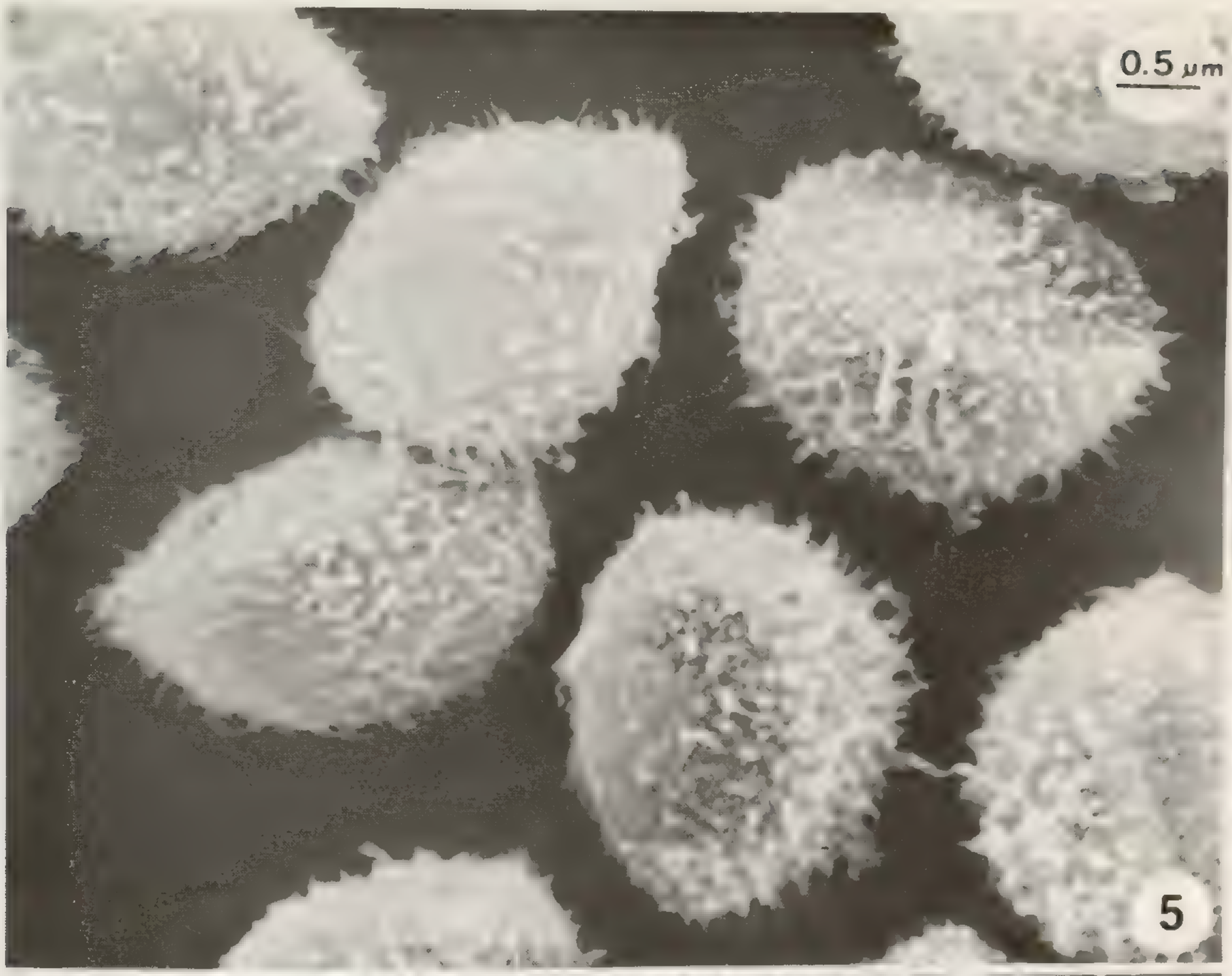
The megaspore of *I. melanopoda* is trilete, indicated by the triradiate scar which, at its point of convergence, identifies the proximal pole that was toward the center of the original tetrad formed by meiosis (*Fig. 1*). Under greater magnification, the perine (the loose outer wall of the spore) appears to be echinate, possessing tapering, pointed projections (*Fig. 3*). The megaspore of *I. butleri* is also trilete, but shows an arachnoid or cobwebby perine, thus readily distinguishing the two species (*Figs. 2* and *4*).

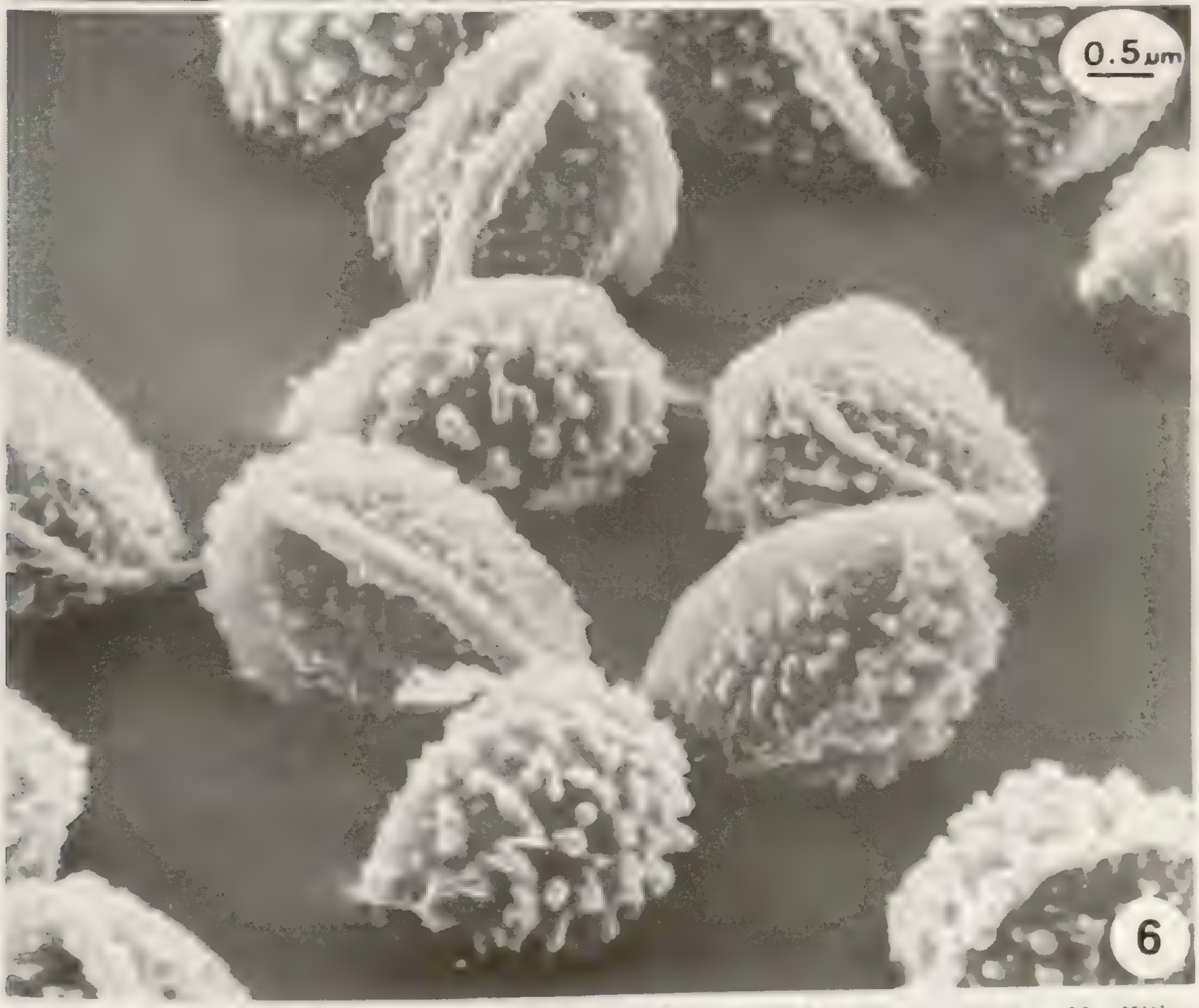
The microspores of *I. melanopoda* and *I. butleri* are even more distinct than the megaspores. On *I. melanopoda* microspores, the trilete or monolete scar apparently is concealed beneath a densely echinate perine, whereas in *I. butleri*, the microspores are markedly trilete with a baculate to verrucate perine (*Figs. 5* and *6*).

Engelmann (1882) recognized the taxon *I. melanopoda* var. *pallida*, which was based on plants collected in wet, pine woods in Houston, Texas. This collection consists of large, robust specimens lacking the black leaf bases of var. *melanopoda*. Pfeiffer (1922, p. 151) found that these specimens do not exceed northern forms in spore size, leaf number, or leaf length. Furthermore, it has been observed by a number of collectors that var. *pallida* often occurs sporadically throughout any given population of *I. melanopoda*, and therefore should be accorded form rather than varietal status. It is interesting to note that a Vasey collection taken at Clinton, Iowa (MO 1852300) and labeled as an isotype of var. *melanopoda* consists of four plants, one of which is forma *pallida*. Viewed under the SEM, spores of *I. melanopoda* f. *pallida* (Engelm.) Clute show surface features characteristic of *I. melanopoda* f. *melanopoda*.

Engelmann (1882) also recognized *I. butleri* var. *immaculata*, a somewhat intergrading variety which, according to Pfeiffer (1922), combines the fine leaf habit of *I. butleri* with the greater leaf length and stronger corm development of *I. melanopoda*. In addition, the range in spore size is said to be intermediate, varying from 400 to 500 μm in diameter. SEM examination of the spores of var. *immaculata* indicates that its spore surfaces closely conform to those of *I. butleri*.

With these differences between both the megaspores and the microspores of *I. melanopoda* and *I. butleri* established, we examined spores of somewhat intermediate material from southern Illinois and from Magazine Mountain and Petit Jean Mountain in Arkansas. Without a doubt, all of it is *I. melanopoda*. Therefore, *I. butleri* should be deleted from the Illinois flora.





Isoëtes microspores. FIG. 5. *I. melanopoda*, Giant City State Park, Jackson Co., IL, *Wilson 2434* (SIU). FIG. 6. *I. butleri*, Limestone glade, Newton Co., AR, *Taylor 1228* (SIU).

All the southern Illinois and the two Arkansas stations for *I. melanopoda* are on moist layers of thin soil in depressions on sandstone cliffs. Since no manuals have indicated such a terrestrial habitat for this species, which usually occurs in wet depressions in lowland habitats, Voigt (1953) reported an Illinois collection of *I. melanopoda* as *I. butleri*. Mohlenbrock (1955, 1967, p. 38) maintained *I. butleri* in the Illinois flora and added several county records. True *I. butleri*, unlike most *I. melanopoda*, shows a definite affinity for drier, upland sites, but more often calcareous, rather than sandstone ones. The relative rarity of this habitat in Illinois makes the discovery of *I. butleri* in the state unlikely.

The authors wish to express their thanks to Dr. Delzie Demaree and Dr. Jewel Moore for their help in locating the Arkansas specimens used in this study, and to Mr. Keith Wilson who supplied living material from southern Illinois.

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REVIEW

"THE CALIFORNIA SPECIES OF ASPIDOTIS," by Alan R. Smith, Madroño **23:** 15–24. 1975.—Taxonomic uncertainty has plagued the species placed, since the time of Copeland's "Genera Filicum," in *Aspidotis*. Smith's paper includes data from chromosomes, flavenoid chemistry, habitat (especially rock substrate), geographic range, sporophyte and spore morphology, and spore germination and gametophyte growth on different substrates. The data reveal that there are two basic diploid species in California, *A. densa* and *A. californica*. The latter has a previously undetected tetraploid race. The third California species, *A. carlotta-halliae*, is also tetraploid and is the hybrid of diploid *A. californica and A. densa*. The parental species grow on different substrates. They occur at similar altitudes in the Coast Ranges, but are separated altitudinally in the Sierra Nevada. Known hybrids, needless to say, are all from the Coast Ranges. The origin of the tetraploid cytotype of *A. californica* is still unknown. Data for the study were compiled by students as a seminar project under Dr. Smith's direction. It is heartening to see multifaceted investigations prove so fruitful. The approach deserves to be emulated by others working with temperate North American ferns.—*D.B.L.*

Gametophyte Sex Expression in Some Species of Dryopteris[1]

MICHAEL I. COUSENS*

The study of sexuality in fern gametophytes has stimulated research in the genetic consequences of gametophyte sex expression (Klekowski, 1971) and in the physiology of sex determination in ferns (Doöpp, 1950; Voeller, 1971). A class of antheridia-inducing hormones, antheridogens, has been discovered in several genera of ferns including *Dryopteris* (Doöpp, 1950; Voeller, 1964). Homosporous ferns differ fundamentally from heterosporous plants in their potential for intragametophytic selfing, which eliminates heterozygosity by the union of genetically identical egg and sperm derived mitotically from a single gametophyte (Klekowski & Lloyd, 1968). Homeologous pairing in polyploids is a possible mechanism for expression of heterozygosity following intragametophytic selfing (Klekowski & Hickok, 1974). Intragametophytic selfing and intergametophytic crossing are genetically equivalent to self pollination and cross pollination in heterosporous plants.

The occurence of bisexual, male, and female gametophytes in multispore cultures of *Dryopteris ludoviciana* suggested that gametophytes of this genus are not regularly bisexual (Cousens & Horner, 1970). This paper extends the observation of gametophyte sex expression to seven additional species of *Dryopteris*. Various patterns of sex expression may be adaptive in allowing different balances of intra- and intergametophytic mating in different environments (Klekowski, 1972).

Dryopteris is a large genus of ferns notable for frequent hybridization between species (Wagner, 1970). Three tetraploid species studied, *D. campyloptera, D. spinulosa,* and *D. celsa,* probably arose by chromosome doubling of sterile hybrids; their ancestral taxa are either known or hypothesized (Wagner, 1970; Walker, 1961, 1962). *Dryopteris clintoniana* is a hexaploid hybrid of *D. goldiana* and *D. cristata* (Wagner, 1970). *Dryopteris intermedia, D. goldiana, D. marginalis,* and *D. ludoviciana* are all sexual diploids.

Cultures of *Dryopteris* gametophytes were initiated by inserting a sterile wooden applicator into 25 ml spore vials and transferring 400–600 adherent spores to a 5 ml beaker which was then filled with sterilized water to which a trace of detergent had been added. Each species studied was represented by spore samples from two or more sporophytes. After the spores were dispersed in the liquid, the suspension was divided among three sterile 60 mm petri dishes filled with sterile clay–loam soil. Only cultures which resulted in a gametophyte population density of 1–3 gametophytes per cm^2 were used because previous work has shown that culture density modifies sex expression (Cousens & Horner, 1970; Rashid,

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[1]This work was initiated during the Highlands Pteridology Conference, June 1970, and was completed with support of an NDEA predoctoral fellowship to the Botany Department, Washington State University. The author thanks F. S. Wagner, W. H. Wagner, Jr., and D. Whittier for their generous contribution of *Dryopteris* spores and vouchers.

1970). The numbers of gametophytes were sufficient so that the removal of some for sampling did not modify population density significantly.

Cultures were maintained in a growth chamber at 21 ± 2°C and were illuminated by fluorescent and incandescent bulbs at an intensity of 350–400 ft-c for 14 hours daily. The cultures were watered with sterilized water twice weekly. Twenty-eight or more gametophytes were harvested at intervals from 25 to 106 days after sowing. They were then cleaned, stained in warm acetocarmine, and mounted in Hoyer's medium (Beeks, 1955). After curing on a slide warmer at 35°C for ten days, the presence of archegonia and antheridia on individual gametophytes was recorded. The mean sex expression values for each species are listed in *Table 1*, which includes data from similar cultures of *D. ludoviciana* (Cousens, 1969).

TABLE 1. GAMETOPHYTE SEX EXPRESSION IN *Dryopteris*.

Species	*Ploidy*[1]	*Age in Days*	*Sample Size*	*% Asexual*	*%* ♀	*%* ♂	*%* ♀	*Sporophyte Number*
D. intermedia	2x	85	115	0	13	17	70	4
D. spinulosa	4x	81	41	0	14	27	59	3
D. goldiana	2x	104	42	0	17	22	61	3
D. clintoniana	6x	98	29	0	44	44	12	2
D. celsa	4x	90	31	0	45	26	29	4
D. campyloptera	4x	25	33	40	15	6	34	4
D. campyloptera		35	43	0	0	58	42	
D. campyloptera		45	47	4	4	47	44	
D. campyloptera		95	49	0	51	16	32	
D. marginalis	2x	25	50	60	4	28	8	6
D. marginalis		45	57	31	10	42	16	
D. marginalis		106	43	4	40	53	3	
D. ludoviciana	2x	25	30	48	7	11	34	2
D. ludoviciana		35	36	30	28	2	40	
D. ludoviciana		45	28	25	36	0	39	
D. ludoviciana		58	58	19	15	40	26	
D. ludoviciana		72	48	19	10	31	40	

[1]Data from Wagner (1970)

All eight species studied had bisexual, male, and female gametophytes, but the proportions of the three differed widely in different species (*Table 1*). The sex expression data taken at successive intervals for *D. campyloptera*, *D. marginalis*, and *D. ludoviciana* confirmed the observation that the sex expression of a sample changes with culture age (Klekowski, 1970; Rashid, 1970).

Although several patterns of gametophyte sex expression were found, these can be divided first into those with a low percentage of bisexual plants (*D. intermedia*,

D. spinulosa, *D. goldiana*, and *D. ludoviciana*) and those with a moderate percentage of bisexual plants (*D. clintoniana*, *D. celsa*, *D. campyloptera*, and *D. marginalis*). The percentage of bisexual plants is best assessed at the oldest comparable interval because some male and female gametophytes regularly become bisexual with age. *Dryopteris clintoniana* and *D. marginalis* are alike in having a high proportion of male gametophytes, whereas *D. campyloptera* and *D. celsa* have a lower percentage of male gametophytes.

In addition to the pattern noted above, a distinct pattern of sex expression is shared by *D. intermedia*, *D. spinulosa* (which incorporates a *D. intermedia* genome), and *D. goldiana*. Bisexual plants range from 13–17%, male plants range from 17–27%, and female plants range from 59–70% (*Table 1*). The pattern of sex expression does not correlate with genome: *D. goldiana* does not share a genome with *D. intermedia* or *D. spinulosa* and differs in pattern of sex expression from *D. celsa* and *D. clintoniana*, species with which it does share a genome.

The pattern of sex expression for *D. intermedia*, *D. spinulosa*, *D. goldiana*, and *D. ludoviciana* suggests a low frequency of intragametophytic selfing since this can occur only on bisexual gametophytes. The higher percentage of bisexual gametophytes in cultures of *D. clintoniana*, *D. celsa*, *D. campyloptera*, and *D. marginalis* suggests a higher potential for intragametophytic selfing, although a bisexual gametophyte is not obliged to self.

Sex expression pattern may respond adaptively in the *Dryopteris* species studied, but it remains to be determined whether such selection is acting on alleles that directly determine part of the pattern of sex expression, or on alleles that indirectly determine the pattern of sex expression by controlling the production of antheridogen or an antheridogen-like substance. Alleles that directly determine sex expression pattern could best be discovered through sex expression data for single spore cultures that would be free of the antheridium-inducing effects of a complex gametophyte population. The limited data available for gametophytes isolated after germination in multi-spore cultures fail to confirm a Mendelian pattern in *Dryopteris ludoviciana* (Cousens & Horner, 1970) or in *Pteridium aquilinum* (Näf, 1958).

Where sex expression data and genetic data are available for other genera, sex expression systems initially adapted for outcrossing usually correlate well with a high level of genetic load, which prevents the production of viable sporophytes following intragametophytic selfing (Klekowski, 1970, 1972). Where the pattern of sex expression favors intergametophytic mating throughout the period of culture (as in the Blechnaceae), genetic tests are mostly consistent with the hypothesis that a reduced percentage of bisexual gametophytes reflects frequent intergametophytic mating, as suggested by a high level of heterozygosity for sporophytic lethals (Cousens, 1973; Klekowski, 1969).

In addition to the obvious evolutionary advantage of a sex expression pattern which allows the accumulation of heterozygosity, it is possible that hybridization between *Dryopteris* species may have increased as a result of unisexuality in *Dryopteris* gametophytes. Thus, variable sex expression in the genus may lead to both divergent and reticulate evolution.

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Photosynthesis and Respiration Rates of Ferns

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In contrast to the large amount of information available concerning rates of photosynthesis and respiration in flowering plants, very few studies of this sort have been made with ferns. Previous investigations of photosynthesis and respiration in ferns include those of Johansson (1923, 1926), Böhning and Burnside (1956), Starzecki (1958, 1959) and the recent study of Hew and Wong (1974).

The present investigation is concerned with the chlorophyll content, stomatal numbers and distribution, Hill reaction activity, light compensation points, light saturation intensities, and rates of photosynthesis and respiration in six species of ferns, three from shady habitats and three which grow in full sunlight.

The species studied were *Asplenium platyneuron* (L.) Oakes, *Botrychium virginianum* (L.) Swartz and *Woodsia obtusa* (Spreng.) Torr., which were collected from shady habitats, and *Botrychium dissectum* f. *obliquum* (Muhl.) Fern., *Pellaea atropurpurea* (L.) Link, and *Polypodium polypodioides* var. *michauxianum* Weatherby, which grow in situations exposed to full sunlight. The plants were collected in the field and transplanted to comparably shaded or lighted situations in the greenhouse two to three weeks prior to photosynthetic measurements.

METHODS

Chlorophyll Analyses.—The method of the Association of Official Agricultural Chemists (1950) was used. The pigments were extracted by grinding a 5 g sample of fresh leaf tissue in 50 ml of 80% aqueous acetone in a Waring blendor. The acetone solution of pigments was freed of leaf debris by suction filtration. The pigments were transferred to ether in a separatory funnel, and the ether layer, after washing with water and drying with anhydrous Na_2SO_4, was then made up to a volume of 100 ml. Absorbance determinations were made at 642.5 nm and 660 nm using a Beckman DU spectrophotometer.

Stomatal Density and Distribution.—Fresh green fronds were first covered with toluene to remove the cuticle. Then a viscous plastic (Archer, 1950) was applied and allowed to dry for 5–10 minutes. The dried plastic from six fronds of each species was peeled off and examined. Five fields per frond were selected for counting, giving a total of 30 fields per species. Stomatal counts were made from the plastic impressions, and are reported as numbers of stomata per cm^2.

Hill Reaction.—Chloroplasts were isolated using the method of Granick (1938). A portion of leaf tissue was ground in 0.5M sucrose solution in a Waring blendor at 4° for 30 seconds, filtered through cheesecloth, and differentially centrifuged, first at 100 × g and then at 1000 × g. The reactions were carried out at a light

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intensity of 4,000 ft-c in 25 ml Erlenmeyer flasks containing 8.0 ml of reaction mixture, consisting of 1.0 ml of 2,6-dichlorophenolindophenol (0.2 mg/ml), 0.2 ml of the chloroplast suspension, and 6.8 ml of distilled water. A dark control was included to insure that reduction of the dye occurred only in the light. The optical density changes at 600 nm concomitant with the reduction of the dye were followed with a Beckman DU spectrophotometer. Readings were taken at initial time and at 1 and 2 minutes. The chlorophyll content of the suspension was then determined according to Vishniac (1957). The Hill activity was expressed as μM of dye reduced/min/mg chlorophyll.

Photosynthetic Measurements.—The apparatus used included a Beckman Model 15A L/B Infrared Carbon Dioxide Analyzer and a plant chamber (capacity 6.43 l) through which air was circulated at a constant rate of 0.1 cu ft/min by means of a Thiberg Model 1 aerator pump. Water from a thermostatically controlled water-bath was circulated through the double wall of the plant chamber to insure a constant temperature. Illumination was provided by a General Electric 750 watt lamp placed 12 inches above the lucite top of the plant chamber. A rheostat was used to control light intensity. Illumination intensities were measured with a Weston Model 756 illumination Meter (Daystrom, Inc., Weston Instrument Division, Newark, New Jersey). Heating from the light source was minimized by placing a pyrex dish filled to depth of 2 inches with distilled water in the light path. The CO_2 concentration in the plant chamber was recorded with a Brown Electronik 0–10 mv circular recorder (Minneapolis-Honeywell, Brown Instrument Division, Philadelphia, Pennsylvania).

In a typical experiment, the fronds of the fern selected for study were enclosed within the plant chamber, with the rhizome protruding through a hole in the bottom of the chamber. Modeling clay was used to seal this opening, making an airtight, closed system. The CO_2 concentration was atmospheric (ca. 300 ppm) at the start of each run. After a short period of equilibration, apparent photosynthesis was measured for 1 hour. The chamber was then darkened by means of a black cloth placed over the top, and respiration was measured for 1 hour. Data are expressed in terms of mg CO_2/hr/dm^2. Leaf areas were determined after each experiment using blueprint paper and by weighing.

Photosynthesis was measured at a series of light intensities ranging from 50 to 5,000 ft-c, and at a variety of temperatures. The optimal temperature for photosynthesis was determined for each fern species, but because of the great variation among species, it was decided to make all subsequent measurements at only two temperatures, 18° and 30°C. The data presented are based on a series of such experiments with three individual plants of each species.

RESULTS

Chlorophyll Analyses.—*Table 1* contains data on the amounts of chlorophylls. There was a much greater quantity of chlorophylls in the shade species (2.21–2.74 mg/g fr wt) than in the sun species (1.03–1.42 mg/g fr wt). The chlorophyll *a*/*b* ratio, which ranged from 2.1:1 to 2.7:1, was slightly higher in the sun ferns than in the shade species.

Stomatal Number and Distribution.—Data for stomatal density and distribution are presented in *Table 2*. Stomata were confined to the lower epidermis except in *B. dissectum*, which had a few scattered on the upper epidermis. In the shade species the stomatal number ranged from 3,200/cm^2 to 4,900/cm^2, whereas in the sun species the number ranged from 6,500/cm^2 to 7,400/cm^2. The data clearly illustrate a relation between stomatal number and habitat.

Hill Reaction.—*Table 2* also includes data for Hill reaction activity, which in shade species ranged from 14.9 to 16.6 μM DPIP reduced/min/mg Ch, but in the sun species ranged from 18.9 to 24.8 μM DPIP reduced/min/mg Ch. Hill reaction activity was thus considerably higher in the sun species than in shade ferns.

TABLE 1. CHLOROPHYLL CONTENT OF SIX FERNS.

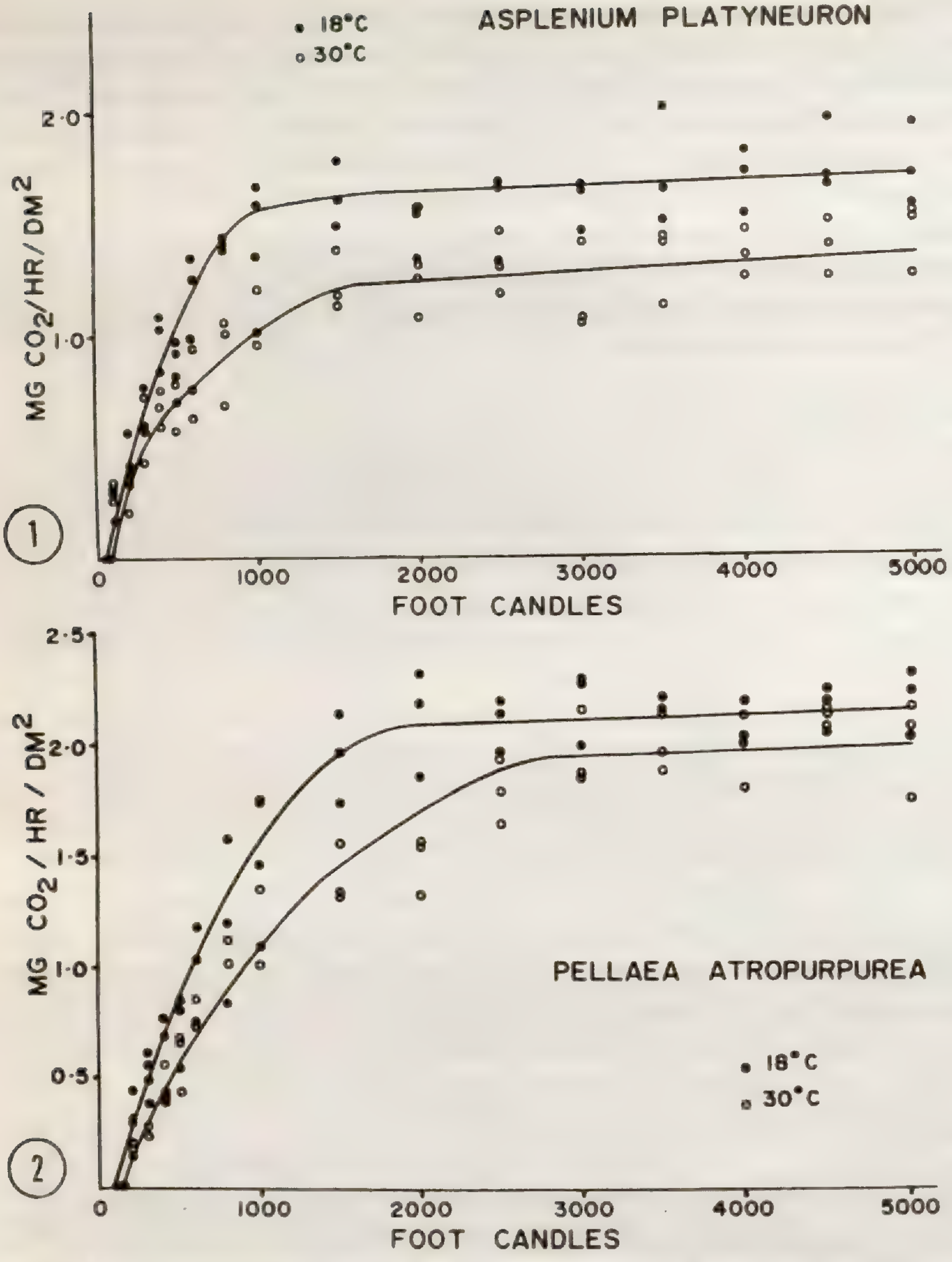
Species	*Chlorophyll a* (mg/g fr wt)	*Chlorophyll b* (mg/g fr wt)	*Chlorophyll a + b* (mg/g fr wt)	*Chlorophyll a/b ratio*
SHADE				
Asplenium platyneuron	1.90	0.82	2.72	2.3
Botrychium virginianum	1.88	0.86	2.74	2.1
Woodsia obtusa	1.56	0.65	2.21	2.4
SUN				
Botrychium dissectum	1.26	0.50	1.76	2.5
Pellaea atropurpurea	1.04	0.38	1.42	2.7
Polypodium polypodioides	0.75	0.28	1.03	2.7

TABLE 2. STOMATAL NUMBER AND HILL REACTION ACTIVITY IN SIX FERNS.

Species	*Stomata/cm^2 of epidermal surface*		*Hill Reaction Activity*[1]
	Upper	*Lower*	
SHADE			
Asplenium platyneuron	0	4,900	14.9
Botrychium virginianum	0	3,200	16.6
Woodsia obtusa	0	3,200	16.6
SUN			
Botrychium dissectum	2	7,400	24.8
Pellaea atropurpurea	0	6,700	18.9
Polypodium polypodioides	0	6,500	23.4

[1] μM DPIP reduced/min/mg of chlorophyll.

Photosynthetic Measurements.—*Figure 1* illustrates the light saturation curve for gross photosynthesis of the shade fern *A. platyneuron*. It can be seen that the maximum photosynthetic rate at 18° is higher than at 30° and that light saturation of photosynthesis occurs at 1000–1500 ft-c. The light saturation curves of the other two shade species, *B. virginianum* and *W. obtusa*, were very similar to this. *Figure 2* represents the light saturation curves for gross photosynthesis of the sun fern *P. atropurpurea*. Little difference in the rates of gross photosynthesis at the two temperatures, at least at the higher light intensities, was noted in the sun ferns, except in the case of *B. dissectum*, in which photosynthesis was considerably decreased at 30°.



FIGS. 1–2. Light saturation curves for gross photosynthesis at 18°C and 30°C. FIG. 1. *Asplenium platyneuron*. FIG. 2. *Pellaea atropurpurea*.

Table 3 includes photosynthetic data for all the species studied, both at 18° and 30°. There are similarities in light compensation points and light saturation intensities for the species within each group. In the shade species, net photosynthesis was not reduced to zero until light intensities as low as 50 to 100 ft-c were reached. In the sun species *P. atropurpurea* and *P. polypodioides*, net photosynthesis was zero at light intensities of 100 to 150 ft-c, and light saturation was attained in the range of 2,000 to 2,500 ft-c. In *B. dissectum*, however, which had light saturation intensities of 1,500–2,000 ft-c, the compensation points were also lower than in the other sun species.

Light saturation intensities of the shade species at either temperature were less than those of the sun species. The same is true of the light compensation points, with the exception of *B. dissectum*. Both light compensation points and light saturation intensities of all species were higher at 30° than at 18°. The apparent photosynthetic rates of the shade species were about the same as in *P. polypodioides*, but less than those of the other two sun species. Photosynthetic measurements taken of some shade plants of *P. polypodioides* were found to be much lower than in the sun plants of this species.

TABLE 3. OPTIMAL TEMPERATURE FOR PHOTOSYNTHESIS, LIGHT COMPENSATION POINT, LIGHT SATURATION INTENSITY, AND MAXIMUM RATE OF APPARENT PHOTOSYNTHESIS FOR SIX FERNS.

Species	*Optimal Temp.* (°C)	*Light Comp. Point* (°C)	(ft-c)	*Light Saturation* (ft-c)	*Apparent Photosynthesis* (mg CO_2/hr/dm²)
SHADE					
Asplenium		18°	50	1000	1.45
platyneuron	21°	30°	75	1500	1.05
Botrychium		18°	50	800	1.46
virginianum	15°	30°	100	1000	1.19
Woodsia		18°	50	1000	1.61
obtusa	24°	30°	75	1500	1.43
SUN					
Botrychium		18°	50	1500	2.02
dissectum	18°	30°	75	2000	1.61
Pellaea		18°	100	2000	1.83
atropurpurea	27°	30°	150	2500	1.71
Polypodium		18°	100	2000	1.41
polypodioides	21°	30°	150	2500	1.19

TABLE 4. DARK RESPIRATION RATES OF SIX FERNS.

Species	*Dark Respiration* (mg CO_2/hr/dm²) 18°C	30°C
SHADE		
Asplenium platyneuron	0.18	0.18
Botrychium virginianum	0.23	0.23
Woodsia obtusa	0.22	0.19
SUN		
Botrychium dissectum	0.23	0.27
Pellaea atropurpurea	0.27	0.24
Polypodium polypodioides	0.21	0.26

Table 4 includes the respiratory data at both 18° and 30°. With the three species from shade habitats, no significant difference was observed in respiratory rates at the two temperatures; but in the sun ferns, respiratory rates were higher at 30° than at 18°.

DISCUSSION

Chlorophyll content of the shade species was considerably higher than that of sun species. No correlation of chlorophyll content with apparent photosynthetic rate was found; the shade species with higher chlorophyll content had lower photosynthetic rates than the ferns from sunny habitats, a result presumably

attributable to a difference in size of the photosynthetic unit in the two cases. The chlorophyll *a/b* ratio was higher in sun than in shade ferns.

Stomatal density was considerably higher in the sun ferns than in the shade species examined. Hill reaction rates showed a good correlation with the observed rates of photosynthesis, being higher in sun species than in shade species.

Light compensation points were lower for the shade ferns than for sun species, and were lower at 18° than at 30°. The same is true of the light saturation intensities permitting maximal rates of photosynthesis.

Rates of apparent photosynthesis in the ferns which we studied are considerably lower than those found in either woody or herbaceous higher plants (Altman & Dittmer, 1964), but are within the lower portion of the range of values for ferns reported by Hew and Wong (1974). Likewise, the optimal temperature for photosynthesis in ferns is lower than for many higher plants, although not so low in our experience as reported by Johansson (1926) or by Hew and Wong (1974). We made no determinations of photorespiration rate, but since Hew and Wong (1974) have shown that photorespiration rate in ferns is generally higher than that of dark respiration, the actual rate of photosynthesis is probably some 50% greater than that of apparent photosynthesis.

Rates of dark respiration in the shade ferns we studied showed no acceleration at 30° over that at 18°. An increase in dark respiration at the higher temperature was shown, however, by two of the three ferns studied characteristic of sunny habitats. Hew and Wong (1974) reported that the rates of dark respiration in the ferns which they studied ranged from one tenth to one fourth of the photosynthetic rate, a finding which is confirmed in our experiments.

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Polypodium vulgare Versus P. virginianum in the Eastern United States

J. M. BEITEL*,[1]

Fosberg's (1968) report of the European *Polypodium vulgare* L. on the coastal plain of the northeastern United States is of significance to the phytogeographical study of the *P. vulgare* complex in North America and Europe.

Fernald (1922) enumerated the main morphological differences between *P. virginianum* L. and *P. vulgare* L. These include an acrid tasting rhizome, scales with sagittate attachment, and submarginal sori in *P. virginianum*, as opposed to a sweet rhizome, peltately attached rhizome scales, and medial sori in *P. vulgare*. The most characteristic feature of *P. virginianum* was found to be the glandular paraphyses described by Martens (1943, 1950) and by Martens and Pirard (1943).

The only other possible report of true *P. vulgare* in eastern North America is a herbarium specimen dealt with by Martens (1943). The plant in question (from the Antwerp Botanical Garden) was mounted on the same herbarium sheet as a plant with paraphyses collected in Philadelphia in 1824. Martens concluded that the non-paraphysate *P. vulgare* specimen had been added to the sheet at a later date from a European locality. No occurrence of *P. vulgare* in eastern North America is mentioned in the works of Manton (1950) or Shivas (1961a, b) on the cytogenetics of the *P. vulgare* complex in Europe, nor by Manton (1950, 1951, 1957), Manton and Shivas (1953), or Evans (1971) in their studies of North American *P. virginianum*. All the aforementioned works stress the separate distributions of *P. vulgare* and *P. virginianum*.

Fosberg, in recording *P. vulgare* from Long Island, Suffolk County, New York, based his identification on the fact that the sori bore no paraphyses, and the habitat—a sandy slope of glacial origin—was one that was more typical of the European species. Fernald (1922) had previously noted that *P. virginianum* is ordinarily a plant of rock habitats, only rarely occurring as an epiphyte; no mention of sandy banks was made. This viewpoint has been repeated by various authors, e.g., Cobb (1956) and House (1924). The question of whether the Long Island *P. vulgare* was indigenous or had been introduced with European trees planted in the area was raised by Fosberg.

In my work on pteridophytes of Suffolk County, I reinvestigated the site of Fosberg's discovery on December 27, 1974, accompanied by G. Paul Kemp. This was made possible by Mrs. Grosvenor Atterbury, the owner, who kindly showed us the location, as she had Dr. Fosberg in 1968. The colony is on the northeast slope of a small glacial hill in the Shinnecock Hills of eastern Long Island at an elevation of ca. 65 ft (not 65 m, as reported earlier). The dominant trees at this

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location are Black Locust (*Robinia pseudo-acacia*), Black Cherry (*Prunus serotina*) and Shadbush (*Amelanchier* sp.), with a tangled underbrush of Arrow-wood (*Viburnum* sp.), Catbriar (*Smilax* sp.), Poison Ivy (*Toxicodendron radicans*), Japanese Honeysuckle (*Lonicera japonica*), Virginia Creeper (*Parthenocissus quinquefolia*), and Bittersweet (*Celastrus scandens*). Several of the cherry trees are large, with trunks 3–4 ft in circumference. The colony of *Polypodium* is about 6 ft in diameter, although it had been several times larger, according to Mrs. Atterbury. Much of the canopy has been opened up by the blowing over of a Shadbush ten inches in diameter, perhaps causing the colony to decrease.

The living plants resemble *P. virginianum*, although the blades are somewhat thinner than usual. Field examination with a hand lens revealed no paraphyses. Several fronds were collected (*Beitel 74229*), as well as a living plant. Subsequent study of the sori under a dissecting microscope, however, revealed a few glandular paraphyses typical of *P. virginianum*, about 4–10 per sorus. The plant in question was determined to be *P. virginianum*, not *P. vulgare*. Normal spores are present without any spore fragments or aborted spores, indicating that the plant is not a hybrid. In order to make certain that this was the same as Fosberg's plant, the original collection (*Fosberg 50490*, US) was examined. It is similar in all respects to *Beitel 74229*, including the paraphyses.

Polypodium virginianum occurs locally in Suffolk County on glacial deposits. Rocky habitats are almost totally absent. The only habitats which offer the drainage apparently required by *P. virginianum* are occasional glacial erratics (large boulders), steep sandy slopes and tree trunks. From the herbarium records of the New York State Herbarium (Albany) and my own collections, it appears that sandy slopes and tree trunks are more common habitats in Suffolk County than are glacial erratics. The only specimen from the latter habitat is "on rocks, woods south of Lily Pond, Southold," September 20, 1925, *Roy Latham s.n.* (NYS). Plants on tree trunks and lower branches are found mostly in areas of high humidity, such as river and stream banks. Although no herbarium records in the New York State Herbarium mention *P. virginianum* occurring epiphytically, I have found it on Red Maple (*Acer rubrum*) along the Nissequogue River in Smithtown and the Carmans River in Southaven and Yaphank. Terrestrial sites exist in Smithtown and in East Hampton. Both are on steep, wooded slopes without any rocks nearby. Herbarium records indicate two such terrestrial localities: Long Beach, Orient Point; and Roanoke Point north of Riverhead, where a large colony of *P. virginianum* over an acre in size grows on steep, sandy banks of the bluffs along Long Island Sound.

In conclusion, true *Polypodium vulgare* has not as yet been demonstrated to occur in eastern North America, and so the geographical separation of *P. vulgare* and *P. virginianum* remains. In addition, *P. virginianum* habitats include not only rocky ledges, boulders, and occasional epiphytic sites, but steep, well-drained, sandy slopes as well. Such sandy slopes provide habitats for the species in areas along the coastal plain and in glaciated regions where rocky habitats are generally lacking.

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REVIEW

"COMPANION TO R. H. BEDDOME'S HANDBOOK TO THE FERNS OF BRITISH INDIA, CEYLON AND THE MALAY PENINSULA," by B. K. Nayar and Surjit Kaur. 1974. $14.00 plus postage.—In less than ten years, Beddome's "Handbook" will be a century old. According to the authors of the "Companion," Beddome's book "is undoubtedly the most important and useful reference on the taxonomy and identity of Indian fern flora." But the advances in fern nomenclature that have occurred since the publication of the "Handbook" have made the names seriously out-of-date. This has been set to rights by Nayar and Kaur in Part I of the "Companion," which is a list in "Handbook" order of the names therein and their modern equivalents. Part II of the "Companion" is a lengthy treatise on the classification of homosporous ferns that Nayar published briefly in Taxon **19:** 229–236. 1970. In the "Companion" the rationale for his system is set forth in full detail. There follows an addendum on revised nomenclature of the thelypteroid ferns, which takes into account R. E. Holttum's work in that area. The work concludes with an index to the names, both in the "Handbook" and its supplement and to those in the "Companion." Anyone who has occasion to use Beddome's "Handbook" will find the "Companion" indispensable. The "Companion" may be purchased from Pama Primlane, The Chronica Botanica, Post Box 123, New Delhi-1, India, or from Otto Koeltz Antiquariat, P. O. Box 129, D-624 Koenigstein/Taunus, West Germany.—*D.B.L.*

Phloem Structure and Development in Blechnum orientale[1]

R. L. FOTEDAR and J. J. SHAH*

In recent years, phloem structure and development in vascular cryptogams have received much attention. Among the genera that have been studied are: *Selaginella* (Burr & Evert, 1973), *Polypodium* (Evert & Eichhorn, 1973), *Isoëtes* (Kruatrachue & Evert, 1974), *Microsorium* and *Psilotum* (Sakai & Lamoureux, 1973), *Cyathea* and *Pteris* (Shah & Fotedar, 1974 a, b), and *Lycopodium* (Warmbrodt & Evert, 1974). Indian vascular cryptogams have received scant attention in this regard and require investigation.

MATERIALS AND METHODS

Blechnum orientale L. was collected from the Pachmarhi Hills, Madhya Pradesh, India, and was fixed in FAA, 4% formalin solution (Sass, 1958, p. 15) or 3% glutaraldehyde in phosphate buffer at pH 6.8 (Feder & O'Brien, 1968). The material was dehydrated in a TBA series, infiltrated, and embedded in "Tissue Prep." Sections 6–8 μm thick were stained following Cheadle, Gifford, and Esau (1953). Some sections were stained with Regaud's hematoxylin and fast green. The proteinaceous nature of the spherules was confirmed by mercuric bromphenol blue (Mazia, Brewer & Alfert, 1953). Also used were: I_2KI–H_2SO_4 for cellulose wall thickening, I_2KI for plastids, periodic acid–Schiff's reaction for insoluble polysaccharides, and Azure B for nuclear material (Jensen, 1962, pp. 251–252).

Maceration was done in Jeffrey's solution for about one hour at 40–50°C. After washing with a 5% $NaHCO_3$ solution and running water, the macerated material was stained with Delafield's hematoxylin and mounted in glycerine jelly.

Photomicrographs were taken on a Carl Zeiss Photomicroscope I with planapochromatic objectives using Kodak Panatomic-X film and a yellow filter.

The general structure of the phloem was studied in the stems and mature rachises, and the development of sieve cells was studied in young rachises of circinate fronds. For convenience, mature rachises were divided into basal, middle, and terminal regions, whereas young rachises were divided into coiled and uncoiled regions.

A voucher specimen of *B. orientale* is deposited in the herbarium of Sardar Patel University.

OBSERVATIONS

Stem.—The stem has a typical dictyostele with 4 or 5 meristeles. Phloem surrounds the xylem in each meristele and is separated from the xylem by a layer of parenchyma cells. One to three layers of pericycle and a layer of endodermis surround the phloem.

The phloem consists of sieve cells and phloem parenchyma. Some peripheral sieve cells are oblique (*Fig. 1*). Mature sieve cells are enucleate and have thick

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[1]Research supported by National Science Foundation grant GF-36747 to J. J. Shah.

walls, except at the sieve areas. Protein spherules 0.5–1.0 μm in diameter are dispersed in the parietal cytoplasm of the sieve cells (*Fig. 2*); they appear to be more or less aggregated at the sieve areas (*Figs. 28* and *29*).

The sieve cell walls are richly sculptured with sieve areas, which are either simple or compound. In the latter case, narrow wall partitions are present. Each sieve area has a number of minute pores ca. 0.5 μm in diameter that are either lined or filled with callose (*Figs. 3* and *4*). Occasionally large pores ca. 1.0–1.7 μm in diameter are present on the end walls of the sieve cells, which are oblique to very oblique or rarely transverse.

Many sieve cells (irrespective of their position in the meristele) show lateral wall projections that also have sieve areas on them (*Fig. 29*, darts). Sometimes branched sieve cells are found with large projections at their ends (*Fig. 28*). Forked sieve cells rarely are observed.

The sieve cells are 300–1000 μm long (based on 100 measurements). First-formed sieve cells are narrower (5–10 μm wide) than later-formed ones (12–25 μm wide).

Mature rachis.—From the base to the apex, the rachis has 4–10 vascular strands. The vasculature is of the *Aspidium* type. Each vascular strand has an endodermis and a pericycle of 1–3 cell layers. The phloem is separated from the xylem by a layer of parenchyma cells.

The phloem consists of sieve cells and phloem parenchyma cells. Small intercellular spaces are present between the sieve cells and between the sieve cells and contiguous parenchyma cells. Mature sieve cells are thin-walled and enucleate, with small protein spherules in the parietal cytoplasm (*Figs. 5* and *30*). The end walls are oblique to very oblique.

The limits of the sieve areas are indistinct in mature sieve cells, but are distinct in young sieve cells. Their identity becomes more difficult to ascertain due to absent or scanty callose. The sieve area pores become obscure due to the abundance of protein spherules at the sieve area sites (*Figs. 6* and *30*, arrows).

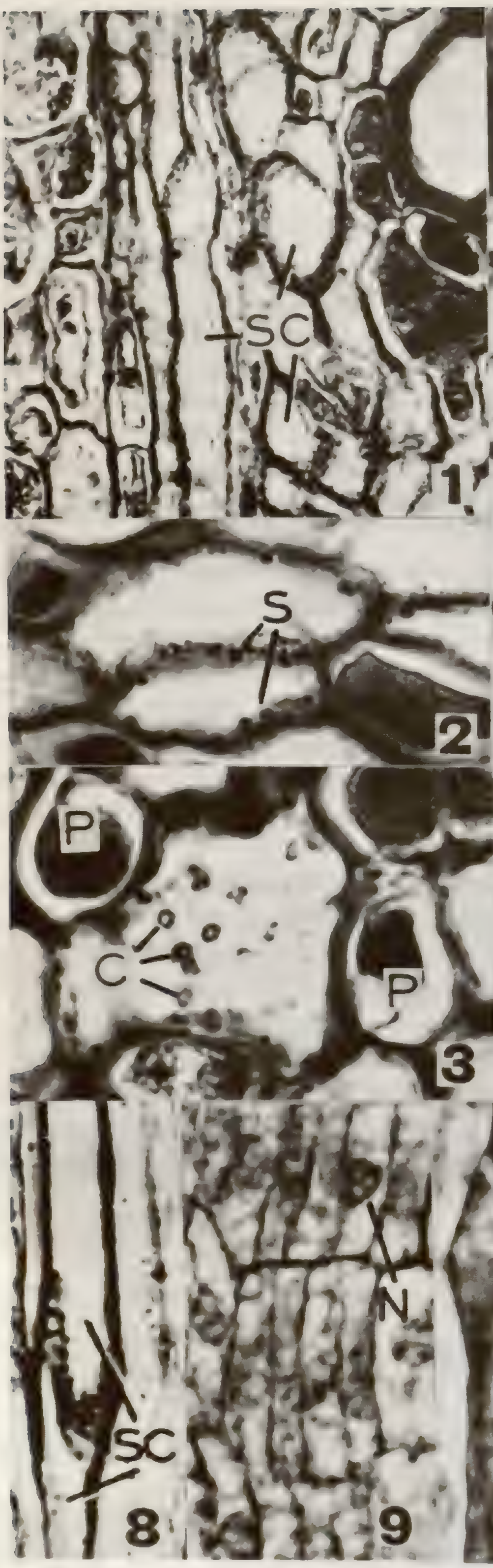
Many sieve cells of the rachis also show lateral wall projections (*Figs. 7* and *30*, dart) similar to those of the stem. Forked sieve cells are rarely observed (*Figs. 8* and *30*). Many first-formed peripheral sieve cells show obliteration, mostly in the basal region of the rachis. The obliterated sieve cells have a narrow lumen and increased callose. Their walls appear thick and stain darkly, probably due to the collapse of the cells.

Sieve cells are 500–1800 μm long (based on 100 measurements). First-formed and later-formed sieve cells are 4–10 μm and 10–20 μm wide, respectively.

Ontogeny.—Sieve cell ontogeny was studied in the young rachis. Sieve mother cells are thin-walled, 20–30 μm long, and ca. 3 μm wide, with transverse end walls. They contain cytoplasm that stains lightly, a round or ellipsoidal nucleus (*Fig. 9*), and 2–4 nucleoli.

Differentiation of the sieve cells, first observed in the adaxial strands, is centripetal. Young sieve cells are solitary or in groups.

Wall Changes.—When the young sieve cells have elongated to ca. 40 μm, their walls become thicker. The thickening is cellulosic. Further wall thickening and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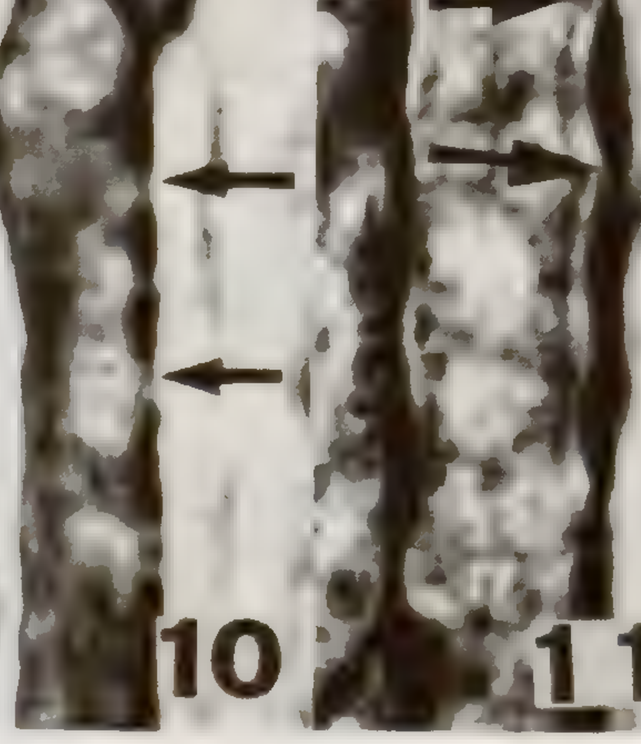
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elongation of the young sieve cells occur more or less simultaneously. The end walls become oblique as elongation of the sieve cells proceeds (*Fig. 10*). Wall thickening remains for a short time after the sieve cells mature, but later the walls appear thin (*Fig. 17*).

Cytoplasm.—Simultaneously with elongation of the young sieve cell, small vacuoles appear in its cytoplasm that become larger during further differentiation (*Figs. 11* and *32*). Minute spherules appear in the cytoplasm (*Figs. 20* and *32*). Initially these do not stain for protein, but with further differentiation of the sieve cells they do. The cytoplasm finally appears as a thin, parietal layer (*Fig. 24*).

Nucleus and Nucleolus.—As the young sieve cells elongate, their nuclei may elongate to ca. 60 μm concurrently. The nuclei may be narrow and thread-like (*Fig. 31*), with pointed (*Fig. 13*) or round (*Fig. 14*) ends. Sometimes the nuclei enlarge but remain spherical.

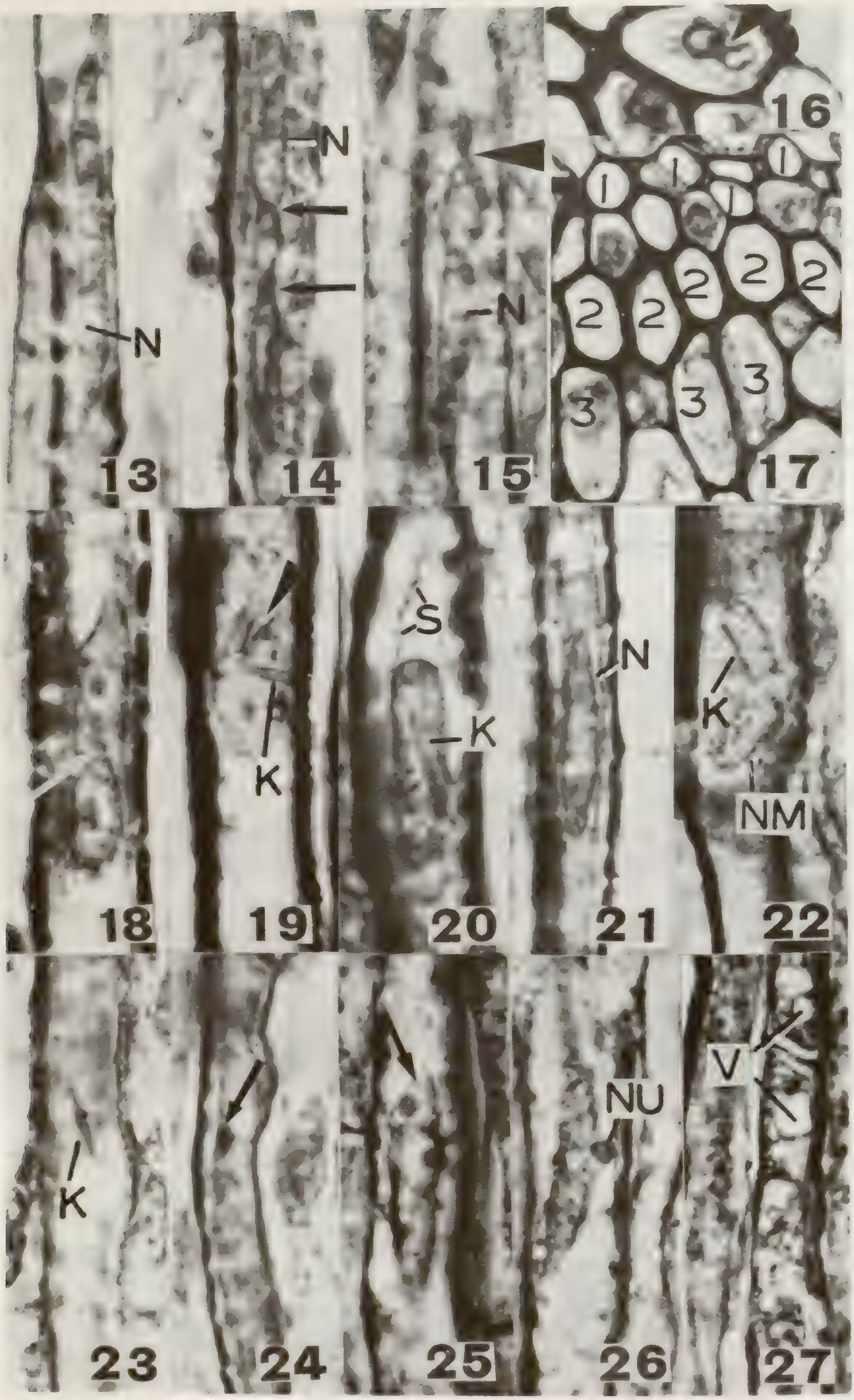
During differentiation of the sieve cells, their nuclei degenerate completely. Elongate nuclei show constrictions (*Figs. 14* and *32*, arrows), deepening of which results in the separation of bits of nuclear material (*Fig. 15*, dart). Lobing (*Figs. 16* and *19*, darts) and twisting (*Fig. 18*, arrow) of nuclei are also seen.

During degeneration, the nuclear contents (except for the nucleolus) appear lightly stained. The nuclear membrane becomes thin and indistinct in places (*Fig. 25*, arrow), probably due to its dissolution or breakdown. Further disintegration of the nucleus results in the release of the nucleolus and dispersion of the nuclear contents into the lumen. This takes place before the cytoplasm appears parietal. Sometimes the nuclear contents disappears first and the nuclear membrane remains distinct (*Fig. 21*), and sometimes the nucleolus is extruded also (*Fig. 26*).

An interesting feature of the sieve cell nuclei is the presence of 1 or 2 rod-shaped, proteinaceous, intranuclear inclusions 5–10 μm long (*Figs. 19* and *20*) called "crystalloides" (Hébant, 1969) or "paracrystals" (Fabbri & Menicanti, 1970). They are released as isolated bodies into the sieve cell lumen (*Fig. 23*), but finally disappear.

Remnants of the degenerated nucleus appear as bits of nuclear membrane (*Fig. 22*) or as darkly staining nuclear bodies (*Fig. 24*, arrow), which also finally disappear.

Blechnum orientale. FIGS. 1–4. Stem. FIG. 1. Transection showing oblique and normal orientation of sieve cells, × 425. FIG. 2. Transection showing sieve cells with protein spherules, × 1140. FIG. 3. Transection showing callose-lined pores at sieve cell end wall, × 1140. FIG. 4. Longisection showing lateral wall sieve area with callose filled pores, × 1700. FIGS. 5–8. Mature rachis. FIG. 5. Transection showing sieve cells with protein spherules and cytoplasm, × 1300. FIG. 6. Longisection showing sieve cell with aggregated protein spherules (arrows), × 1600. FIG. 7. Longisection showing sieve cell with a lateral wall projection (dart), × 1600. FIG. 8. Longisection showing two sieve cells end to end, the lower one forked, × 600. FIGS. 9–12. Young rachis. FIG. 9. Longisection showing phloic procambial cells, × 1100. FIG. 10. Longisection showing thick-walled, young sieve cell with primordial pits (arrows), × 1600. FIG. 11. Longisection showing vacuolated cytoplasm and primordial pits (arrows) of a young sieve cell, × 1600. FIG. 12. Longisection showing sieve areas of a young sieve cell in face view, × 1200. C=callose; CY=cytoplasm; K=intranuclear inclusion; N=nucleus; NM=nuclear membrane; NU=nucleolus; P=parenchyma cell; S=protein spherules; SA=sieve area; SC=sieve cell and V=vacuole.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Sieve Areas.—The primordial pits (also called primary pit fields), which become very prominent due to wall thickening in young sieve cells (*Figs. 10* and *11*, arrows), develop into sieve areas. Callose appears before or after nuclear degeneration (*Fig. 12*) at the sites where minute pores ca. 0.5 μm in diameter become visible. All primordial pits do not develop into sieve areas simultaneously. Callose is generally present on the common walls between sieve cells, but sometimes it is also present on the walls adjacent to parenchyma cells (*Fig. 32*). Sieve areas vary in shape and size (*Fig. 33*). The number of pores per sieve area varies from one to many, without any relationship to sieve area size. As soon as the sieve cell walls become thin, the sieve area limits become indistinct.

Phloem Parenchyma.—The phloem parenchyma cells are 50–90 μm long and 9–15 μm wide in the stem and 150–200 μm long and 10–15 μm wide in the rachis, and are arranged in vertical files. In the stem their walls are thinner than the sieve cell walls, whereas in the rachis they are similar to the sieve cell walls in thickness. The end walls are transverse to oblique (*Figs. 27, 32,* and *34*). The cytoplasm stains darkly and is vacuolate (*Figs. 27* and *32*). The nucleus is spherical or slightly elongate, with one or two nucleoli. Sometimes elongate, necrotic nuclei are observed.

Phloem parenchyma cells contain dark yellow or yellowish-brown, amorphous contents or bodies (*Figs. 32* and *34*, darts). Some minute protein granules and PAS-positive, insoluble, polysaccharide granules are also present. Phloem parenchyma cells in young rachises have a few plastids, but no plastids were observed in the phloem parenchyma cells of mature rachises or stems.

Phloem parenchyma cells develop from normal phloic procambium cells. During differentiation, the phloem parenchyma cells also elongate, but their walls do not thicken the way the walls of young sieve cells do.

DISCUSSION

Walls of the young sieve cells in the rachis of *Blechnum orientale* are thick, but are reduced in thickness in mature sieve cells. Evert and Eichhorn (1973) and Warmbrodt and Evert (1974) reported similar wall behavior in *Polypodium schraderi* and *Lycopodium lucidulum*. The reduction in *P. schraderi* is due to a loose, fibrillar network that becomes compact; in *L. lucidulum* it is due to "ero-

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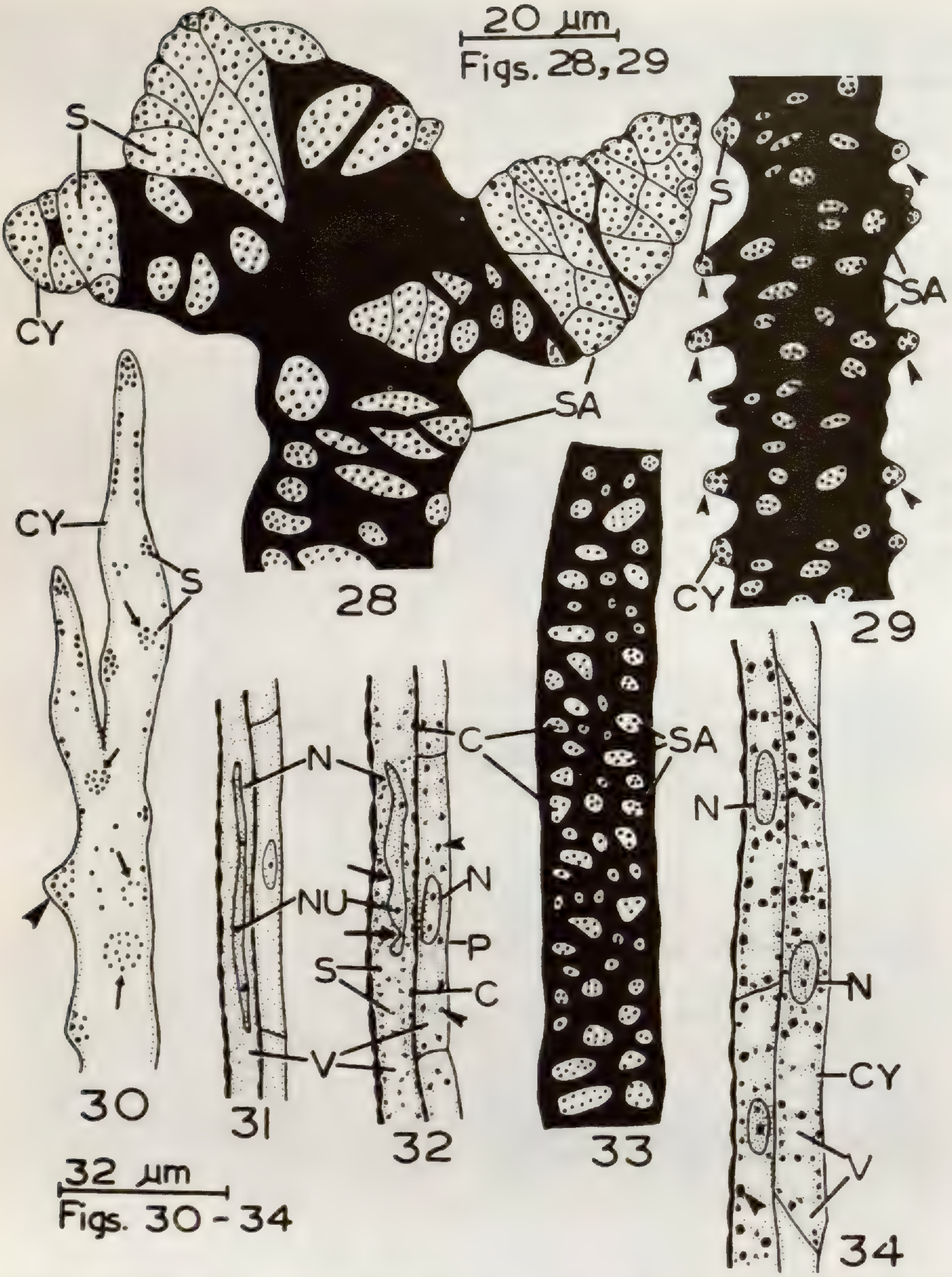
Blechnum orientale. Young rachis. FIGS. 13–26. Sieve cells. FIG. 13. Longisection showing elongated nucleus with pointed ends, × 1700. FIG. 14. Longisection showing elongated nucleus with round ends and constrictions (arrows), × 1700. FIG. 15. Longisection showing detachment of nuclear portion (dart), × 1700. FIG. 16. Transection showing lobed nucleus (dart), × 1600. FIG. 17. Transection showing thin-walled first-formed sieve cells (1), thick-walled recently matured sieve cells (2), and thick-walled young sieve cells (3), × 950. FIG. 18. Longisection showing twisted nucleus (arrow), × 1400. FIG. 19. Longisection showing lobing of nucleus (dart) and intranuclear inclusion, × 1400. FIG. 20. Longisection showing nucleus with two intranuclear inclusions and protein spherules, × 1400. FIG. 21. Longisection showing an empty nucleus, × 1200. FIG. 22. Longisection showing degenerating nuclear membrane bits and intranuclear inclusion, × 1400. FIG. 23. Longisection showing intranuclear inclusion released in the lumen, × 1400. FIG. 24. Longisection showing degenerating nuclear body (arrow), × 1400. FIG. 25. Longisection showing nucleus with thin region of nuclear membrane (at arrow), × 1400. FIG. 26. Longisection showing extruding nucleolus, × 1200. FIG. 27. Longisection showing phloem parenchyma cells with vacuolated cytoplasm, × 1200.



Blechnum orientale. FIGS. 28-30. From maceration. FIG.28. Branched sieve cell of stem showing simple and compound sieve areas. FIG. 29. Sieve cell from stem showing lateral wall projections (darts). FIG. 30. Forked sieve cell of rachis showing lateral wall projection (dart) and aggregated protein spherules (arrows). FIGS. 31-34. Rachis. FIG. 31. Longisection showing elongated sieve cell nucleus. FIG. 32. Longisection showing constrictions (arrows) of sieve cell nucleus; protein spherules in cytoplasm and callose on the wall common with parenchyma cells. FIG. 33. Longisection showing lateral wall sieve areas in face view. FIG. 34. Longisection showing phloem parenchyma cells with vacuolated cytoplasm and dark bodies (darts).

sion" or hydrolysis of wall material. In *B. orientale* it is at least not due to water loss and resultant shrinkage of walls, as mentioned by Esau (1969, p. 61). Mature sieve cells of the stem are thick-walled in *B. orientale*.

Sieve areas develop from primordial pits. Callose appears at pore sites. No scattered pores were observed in *B. orientale*, as they have been in *Pteris longifolia* (Shah & Fotedar, 1974b). Kruatrachue and Evert (1974) report pores only on the end walls of leaf sieve elements in *Isoëtes muricata*. Sieve-tube members have been reported in *Equisetum* species (Lamoureux, 1961) and in *Cyathea gigantea* (Shah & Fotedar, 1974a). In *B. orientale* minute pores are present in end-wall as well as in lateral-wall sieve areas.

The sieve areas are distinct in the stem sieve cells. In the rachis they are distinct in young sieve cells, but become indistinct after the sieve cells mature. We believe this is due to the reduction in wall thickness.

No clumping of chromatic material is observed in the degenerating sieve cell nuclei of *B. orientale*, as has been reported for *Polypodium vulgare* (Maxe, 1966). Intranuclear inclusions similar to those reported here are present in the sieve element nuclei of *Lygodium smithianum, Oleandra distenta, Pityrogramma calomelanos,* and *Microgramma lycopodioides* (Hébant, 1969) and in the mesophyll cells of many other pteridophytes (Fabbri & Menicanti, 1970). As in the mesophyll cells of *B. occidentale* (Fabbri & Menicanti, 1970), the inclusions are proteinaceous in *B. orientale* sieve cells. Upon nuclear degeneration, these inclusions also disappear. Fabbri and Menicanti (1970) believe that these inclusions are formed by the accumulation of proteinaceous material. Their presence in the degenerating nuclei of sieve cells of *B. orientale* can not be explained by this.

Refractive spherules are reported in almost all pteridophytes (Esau, 1969, p. 322), but are absent in *Selaginella kraussiana* (Burr & Evert, 1973), *Isoëtes muricata* (Kruatrachue & Evert, 1974), *Lycopodium lucidulum* (Warmbrodt & Evert, 1974), and *Pteris longifolia* (Shah & Fotedar, 1974b). Similar spherules are present in *B. orientale* sieve cells. We prefer to call them protein spherules, for they are proteinaceous. P-protein is absent in *B. orientale* sieve cells.

Branching and lateral wall projections of sieve elements are reported in *Lycopodium lucidulum* (Warmbrodt & Evert, 1974) and *Ephedra* (Alosi & Alfieri, 1972). They are present in *B. orientale* also, and have sieve areas on them.

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SHORTER NOTES

THE BENJAMIN D. GILBERT FERN HERBARIUM.—The fern herbarium of Benjamin Davis Gilbert, of Clayville, New York (1835–1907), was deposited after his death at Hamilton College, Clinton, New York, where he graduated in the class of 1857. For many years it was available only to those few botanists who knew of its location. The collection was transferred, in 1964, on permanent deposit to the Gray Herbarium, Harvard University, through the interest of Prof. Philip V. Rogers and the Trustees of Hamilton College. The collection consists of about 2500 sheets; an appropriate label has been attached to each so that the integrity of the herbarium is maintained although integrated into the general collections. The herbarium represents not only Gilbert's own collections, mostly from New York and from Jamaica, but also those of a wide range of correspondents in many parts of the world. Among these are sets collected by Jenman in British Guiana, by Alex Moore in Jamaica, by Abraham in Natal, by E. Taylor in Iceland, and by John Muir in California. The single most important part of the collection are the types of the names of new taxa described by Gilbert. These were published, during the period of 1896–1906, mostly in the "Fern Bulletin," the "Bulletin of the Torrey Botanical Club" and in Gilbert's "List of North American Pteridophytes." The purpose of this note is to place on record the present location of the Gilbert Fern Herbarium and of his type specimens.—*Rolla Tryon, Gray Herbarium, Harvard University, Cambridge, MA 02138.*

A NEW LOCALITY FOR BRAUN'S HOLLY FERN IN MINNESOTA.—While mapping the billion-year-old lavas of the North Shore of Lake Superior for the Minnesota Geological Survey in September of 1966, the senior author came upon a very small colony of attractive and unusual ferns in the dark canyon of the Kodonce River (Kadunce Creek) in Cook County, Minnesota (T62N, R2E, Sec 35). Having recently spent several summers in geological field studies in northernmost New Hampshire, he recognized these as Braun's Holly Fern, *Polystichum braunii* (Spenner) Feé var. *purshii* Fern. Since he had not observed this species in several years of field work in Northeastern Minnesota, he recognized its rarity, collected a complete frond and deposited it in the Olga Lakela Herbarium at the University of Minnesota, Duluth. Upon checking the Herbarium and R. M. Tryon's "The Ferns and Fern Allies of Minnesota" (U. of Minn. Press, 1954), it appeared that neither this species nor any other *Polystichum* had ever before been reported in the state. The nearest known locality for *P. braunii* is in the Thunder Bay District of Ontario.

The Minnesota locality is a fascinating gorge 50 to 100 feet deep and 6 to 15 feet across at the bottom, with nearly vertical walls. Cut by a small stream into well-jointed lavas, parts of the canyon are so narrow and blocked by deep pools or waterfalls as to be nearly inaccessible from below. The gorge trends nearly north-south, but because of its depth and narrowness it is cool and shaded much of the day. The *Polystichum* plants were found growing on little shelves and in cracks on the steep east wall above the spring high water line.

The junior author had the opportunity to visit the site in July, 1974. He found plants in the same location and discovered five additional rosettes growing a short distance upstream on a small ledge of the west wall. Except for this restricted colony in the deepest part of the gorge, further searching revealed no new individuals. Companion species growing nearby or in association with *P. braunii* included *Cystopteris bulbifera, C. fragilis, Dryopteris fragrans* var. *remotiuscula, Cryptogramma stelleri, Woodsia alpina* and *W. ilvensis.*—*John C. Green and Daniel R. Engstrom, Dept. of Geology and Dept. of Biology, University of Minnesota, Duluth, MN 55812.*

MICROGRAMMA PILOSELLOIDES WITH FURCATE FERTILE FRONDS.—During a general collection of ferns from the banks of the Río Pacaca near Villa Colón, Province of San José, three populations of *Microgramma piloselloides* (L.) Copel. (*Gómez & Wagner 10131*, CR) were found growing as epiphytes on trees not more than 50 m distant from each other. The three populations were unusual in having a high percentage of furcate fertile fronds (12/38 or 31.6%, 2/29 or 6.9%, and 23/56 or 41.1%). The forking of the fertile blades occurs almost at the base of the fronds, giving rise to two midribs of equal length. There is no evidence of abnormality in the sori, in the density of trichomes, or in sporogenesis; each half of the furcate frond is like any normal, undivided frond. The factors influencing this highly local teratology are as yet unknown.—*Luis Diego Gómez, Herbario Nacional, Museo Nacional de Costa Rica, Apartado 749, San José, Costa Rica.*

A SECOND COLLECTION OF PSILOTUM NUDUM FROM TEXAS.—The Whisk Fern was first recorded in Texas by Donovan S. Correll (Wrightia **2**: 163–165. 1960) as a collection of part of a single plant from Hardin County, two miles south of Saratoga. Lance Rosier, who led Correll to this location, assured him "of other localities in the Big Thicket." But Rosier, now deceased, never disclosed any additional localities.

While conducting an inventory of bog habitats in Freestone County, in the company of Glen Chervenka of the Soil Conversation Service, I discovered a population of *Psilotum nudum* consisting of ten sterile, immature plants 8–12 cm tall. All were found growing within a three square meter area on a seepage slope at the edge of a wet, marshy meadow along a tributary of Mustang Creek about 22 km west of Oakwood. Two specimens, *L. N. Lodwick 216* (MO, TEX), were collected, and verification was by Dr. H. C. Bold, of the University of Texas. The specimens were growing in a wet, peaty humus 5–8 cm deep underlain by a coarse, white sand which has been mapped as a member of the Queen's City Formation (Geological Atlas of Texas, Palestine Sheet, February 1968). The *Psilotum* was associated with a dense canopy of Post Oak (*Quercus stellata*), Water Oak (*Q. nigra*), and Wax Myrtle (*Myrica cerifera*). *Sphagnum subsecundum* was an intermittent ground cover in suitable microhabitats, but due to the dense shade, little ground cover occurred nearby other than the *Sphagnum*. The only disturbance to the area is grazing by cattle, and it is unlikely that any other disturbance is imminent.

This collection of *Psilotum* is the first recorded for the Post Oak Savannah region of Texas and represents a disjunction of approximately 200 km to the northwest of Correll's collection, which is in the Pineywoods of east Texas.—*Laurence N. Lodwick, Resource Management Section, Texas Parks and Wildlife Department, Austin, TX 78701.*

WOODSIA OREGANA NEW TO KANSAS.—An examination of *Woodsia* specimens on deposit at the herbarium of the University of Kansas revealed that a sheet with four plants had been mistakenly identified as *Woodsia obtusa* (Spreng.) Torr. The specimen data are as follows: Kansas: Lincoln County: 2 miles north and 1 mile west of the Beverly exchange of Interstate 70, growing on north facing outcrops of sandstone, one small colony, 7 June 1968, *L. K. Magrath, J. C. Hays, J. E. Taylor, and B. L. Taylor 4137* (KANU). The plants were easily recognized as *W. oregana* D.C. Eaton var. *oregana* by their dark reddish-brown stipes, indusia composed of glandular articulate hairs and linear lobes, and the presence of sessile glands on the rachis and pinnae. This species was previously known from California, Arizona, and New Mexico north to British Columbia and east to Quebec, Vermont and New York; it is also known from Cimmarron County, Oklahoma. This specimen represents an eastern range extension into Kansas of approximately 200 miles.—*Ralph E. Brooks, State Biological Survey of Kansas, 2045 Avenue A, Campus West, Lawrence, KS 66044.*

THE FERNS OF SAN SALVADOR ISLAND.—For the past three years, Hartwick College students have conducted one-month undergraduate floristic studies on San Salvador Island, The Bahamas. This island is 12 miles long and five miles wide. It is approximately 400 miles east southeast of the southern coast of Florida. Like other small Bahamian islands, it consists primarily of limestone, with "scrub-land" the major vegetation type. Four fern species are new to San Salvador Island, and one species that has been previously reported was relocated.

Acrostichum danaeifolium Langsd. & Fisch. was collected in brackish soil at the west side of Flamingo Pond (*Fernandez, Gilbert, Roberto*, and *Thornton 115*) and at the southern part of the northwest arm of Great Lake (*Berg*). It was observed along the shoreline of the southwest portion of Little Lake. All three of these locations are on the northwest part of the island.

Asplenium dentatum L. was found only in the shaded portion of several limestone sink-holes, approximately 10–20 feet deep, located on a rise overlooking Sandy Point on the southwest part of the island (*R. R. Smith, K. Karmen*).

Nephrolepis exaltata (L.) Schott is the rarest San Salvador fern. Only one plant, hence not collected, was found on the upper part of a limestone sink-hole in the same general area as the *Asplenium*.

Pteridium caudatum (L.) Maxon was found at one location on the island, along a trail on the hill in scrub-land south of Flamingo Pond (*R. R. Smith*).

Thelypteris normalis (C. Chr.) Moxley is the only fern previously reported from San Salvador Island. Britton and Millspaugh cited it in "The Bahama Flora" as *Dryopteris normalis* from Watling's Island, an earlier name for San Salvador Island. In Cockburn Town there are two locations, one in a small cave near the northern edge of the town and the other in an abandoned well. A third site was discovered approximately four miles south of Cockburn Town in a limestone pit or quarry near Sugar Loaf (*R. R. Smith*).

The collections cited are deposited in the Herbarium of the University of Florida, Gainesville, Florida (FLAS). Duplicates are in the Hoysradt Herbarium of Hartwick College (HHH), Oneonta, New York. I wish to acknowledge Dr. W. W. Payne and Dr. D. B. Ward for access to the Herbarium of the University of Florida, during the preparation of this paper.—*Robert R. Smith, Department of Biology, Hartwick College, Oneonta, NY 13820.*

POLYPODIUM PLUMULA IN THE BAHAMAS.—To be added to the 36 known species of pteridophytes that I reported as being in the Bahama Islands (including Caicos and Turks islands) in the American Fern Journal **64:** 97–98. 1974 is *Polypodium plumula* Humb. & Bonpl. ex Willd. Its collection data are: North Andros, on walls of north-facing ledges in coppice-covered area of "haystack" hill about 3 miles west of Stafford Creek, along Queen's Highway, December 14, 1974, *D. S. Correll & Don Evans 43960* (FTG, NY, TEX, US).—*Donovan S. Correll, Fairchild Tropical Garden, Miami, FL 33156.*

Suggestions to Contributors

Manuscripts should follow recent Journal style and should be prepared in accordance with the AIBS (1964) "Style Manual for Biological Journals" or the AIBS (1972) "CBE Style Manual." For major articles with more than one literature reference, use the "name and year" system for bibliographic references and the American Standards Association list of bibliographic abbreviations (AIBS, 1964, pp. 82–87), which may be supplemented by the list of Schwarten and Rickett (1958), or by those in the comprehensive "Botanico-Periodicum-Huntianum" (Lawrence et al., 1968). Put a single reference in a footnote or in the text. For shorter notes and reviews, put all references in parentheses in the text. Abbreviations of the names of herbaria should follow the list of Holmgren and Keuken (1974).

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Dryopteris celsa and D. clintoniana in New Jersey

JAMES D. MONTGOMERY*

Since the publication of "The Ferns of New Jersey" by Chrysler and Edwards (1947), a great deal has been learned about the relationships of the eastern American Wood Ferns, *Dryopteris*. The work begun by Manton (1950) has been followed up by Walker (1959, 1961, 1962), and especially by Wagner and his coworkers (1971 and other references). Although some problems still remain to be resolved, the relationships are reasonably well understood (Wagner, 1971). Except for *D. celsa*, the distributions of the species are generally known, but those of the hybrids (especially those involving *D. celsa* and *D. clintoniana*) are known in local areas only, e.g., Michigan (Wagner & Hagenah, 1962; Wagner, Wagner & Hagenah, 1969), Virginia (Wagner, 1963; Wagner & Wagner, 1966), New York (Wagner & Wagner, 1965), and Ontario (Britton & Soper, 1966).

Dryopteris celsa is primarily a southern lowland plant of the piedmont and coastal plain, although its distribution inland may not be fully known. Isolated populations are known in northern New York and Michigan (Wagner, 1971). *Dryopteris clintoniana*, on the other hand, is a northern and upland plant, and rarely is found south of the Wisconsin glacial boundary (Wagner, Wagner & Hagenah, 1969).

Dryopteris species and hybrids are abundant in the northern part of New Jersey. This area should be one of overlap for *D. celsa* and *D. clintoniana*, since the glacial boundary and the upland–lowland boundary both occur here. Only *D. clintoniana* has been previously reported, except for a publication on material used for chromosome studies by Wagner (1971), in which hybrids involving *D. celsa* were detected. No recent field work involving *Dryopteris* populations has been reported, and no other chromosome counts have been made, hence the presence of *D. celsa* in New Jersey is undocumented. The purpose of this paper, therefore, is to investigate the distribution of *Dryopteris celsa* and *D. clintoniana* in New Jersey.

PROCEDURE

Dryopteris celsa and *D. clintoniana* are very difficult to distinguish on morphological grounds alone. Wagner, Wagner and Hagenah (1969) list several characteristics which they found to be useful in distinguishing these species, but I have found that in New Jersey the plants are so variable that distinction on morphological grounds alone was not possible in all cases. However, a spore size difference has been shown to exist (Crane, 1960; Whittier & Wagner, 1971). Chromosome number is presumably an absolute difference: *D. clintoniana* is a hexaploid with 123 pairs at meiotic metaphase; *D. celsa* is a tetraploid with 82 pairs. Chromosomes are also useful in distinguishing hybrids and determining their parentage.

Population studies in the field were carried out over several years in northern

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New Jersey. Populations of *Dryopteris* were located by several means: from data on herbarium specimens, from areas that looked likely on topographic maps, and from an extensive survey along local roads and railroads. Populations with plants of *D. celsa, D. clintoniana*, or their hybrids were carefully examined and fronds removed from the plants for further study. Plants were also transplanted to a garden for further observation and chromosome studies.

Material for chromosome studies was taken from either wild populations directly or from garden transplants. The latter have the advantage that fronds from which pinnae are taken for cytological examination can be readily collected later to determine spore normality and size. Pinnae from plants were fixed in Newcomer's fluid and stored at ca. 0° C. Chromosome squashes were made in half Hoyer's medium and half acetocarmine solution following the methods of F. S. Wagner (pers. comm.). Suitable material was photographed to aid in drawing and counting from the slides.

FIGS. 1-2. Chromosomes of *Dryopteris*. FIG. 1. *D. clintoniana* (123 II), Greendell, Sussex Co., NJ. FIG. 2. *D.* × *dowellii* (156-160 I + 2-4 II), Greendell, Sussex Co., NJ. Bivalents are solid, monovalents outlined, and two monovalents or one bivalent hatched.

Spores were removed from herbarium material, mounted in Turtox CMC-10 non-resinous mounting medium, and examined with a microscope equipped with an ocular micrometer. If the spores were normal, 25 were measured.

Specimens were examined from the following herbaria: AFS, CHRB, MICH, NY, PH, US, and the Staten Island Museum (SIM). Voucher specimens for field population data and chromosome counts are deposited in the Herbarium of Upsala College (EONJ), with duplicates of all cytological vouchers and most field populations deposited in the Chrysler Herbarium of Rutgers University (CHRB). Duplicates are fronds from the same plant.

The author wishes to thank Dr. W. H. Wagner, Jr. and Dr. F. S. Wagner for their many helpful suggestions during the course of this investigation. Several Upsala College students assisted in the field work, especially Mr. Carl Haefele III. Dr. D. E. Fairbrothers kindly made facilities at Rutgers University available for portions of this research. Financial aid from the Upsala College Faculty Research Fund is acknowledged.

TABLE 1. CHROMOSOME COUNTS OF *Dryopteris celsa*, *D. clintoniana*, AND THEIR HYBRIDS IN NEW JERSEY.

I	II	*Source of material*[1]
	Dryopteris clintoniana	
2	121	25466a, Macopin, Passaic Co.
0	123±2	25466h, Macopin, Passaic Co.
0	123	49359k, Big Spring, Sussex Co.
0	122±1	7963e, Big Spring, Sussex Co.
0	122±1	14547c, Greendell, Sussex Co.
	Dryopteris celsa × *cristata*	
83	40	Gaede 1, Ridgewood, Bergen Co.
94	35	Gaede 2, Ridgewood, Bergen Co.
94	35	Gaede 3, Ridgewood, Bergen Co.
90	37	Gaede 5, Ridgewood, Bergen Co.
84	40	Gaede 7, Ridgewood, Bergen Co.
88	38	Gaede 13, Ridgewood, Bergen Co.
	Dryopteris celsa × *goldiana*	
41	41	Gaede 4, Ridgewood, Bergen Co.
41	41	Gaede 6, Ridgewood, Bergen Co.
41	41	Gaede 8, Ridgewood, Bergen Co.
41	41	Gaede 9, Ridgewood, Bergen Co.
41	41	Gaede 10, Ridgewood, Bergen Co.
43	40	Gaede 11, Ridgewood, Bergen Co.
	Dryopteris clintoniana × *cristata*	
36±2	83±2	25466e, Macopin, Passaic Co.
39–45	80–83	Gaede 12, Ridgewood, Bergen Co.
	Dryopteris clintoniana × *intermedia* (= *D.* × *dowellii*)	
156	3	14547a, Greendell, Sussex Co.
163±2	0	14547b, Greendell, Sussex Co.

[1] Counted by author (voucher at CHRB), unless designated as Gaede; these reported by W. H. Wagner, Jr. (1971; voucher at MICH).

RESULTS AND DISCUSSION

Chromosome counts by the author are given in *Table 1*. Chromosomes from one plant of *D. clintoniana* are shown in *Fig. 1*. Chromosomes from the hybrid *D. clintoniana* × *intermedia* (*D.* × *dowellii*) are shown in *Fig. 2*. Chromosome counts clearly indicated that *D. clintoniana* was the plant found in swamps in northwestern New Jersey. Hybrids involving *D. clintoniana* from this area behave as has been shown in other areas (see Wagner, 1971). No evidence of *D. celsa* was found in these data.

Field population studies and herbarium data confirm the above; most specimens from Morris, Passaic, Sussex, and Warren Counties can be considered typical *D. clintoniana*. There is, however, a series of herbarium specimens from the Triassic Lowlands of Bergen County (the most northeasterly county) that show some morphological differences from the material in the northwestern part of the state. These specimens were collected chiefly by Philip Dowell (see Dowell, 1908), Macy Carhart (see Carhart, 1916), and R. C. Benedict from about 1900 to 1915. The fronds tend to have larger and broader basal pinnae with (where preserved) very dark scales at the base of the stipes. These characteristics suggest *D. celsa*.

TABLE 2. SPORE LENGTH IN *Dryopteris celsa* AND *D. clintoniana*.

Source[1]	*Mean* (μm)	*s.d.*	*Observed range*
Dryopteris clintoniana			
10528j, Macopin, Passaic Co.	64.4	4.3	57.6–72.0
10532f, Macopin, Passaic Co.	70.9	4.2	62.4–79.2
8804a, Andover, Sussex Co.	73.6	5.0	60.0–84-0
66009c, Greendell, Sussex Co.	69.8	4.4	60.0–79.2
66010f, Greendell, Sussex Co.	68.9	4.5	60.0–79.2
J. L. Edwards, Succasunna, Morris Co.	66.7	3.7	60.0–74.4
P. Dowell, 5072, Big Spring, Sussex Co.	80.0	5.0	69.6–91.2
Whittier and Wagner (1971)	69.8	3.1	—
Whittier and Wagner (1971)	69.1	4.3	—
Dryopteris celsa			
P. Dowell, 5853, West Englewood, Bergen Co.	54.7	3.6	48.0–60.0
P. Dowell, 5882a, West Englewood, Bergen Co.	55.9	4.3	48.0–62.4
M. Carhart, 8/22/09, Lodi, Bergen Co.	58.4	3.6	52.8–64.8
Conowingo, Maryland	52.4	3.9	45.6–60.0
Conowingo, Maryland	59.0	3.7	52.8–67.2
Whittier and Wagner (1971)	55.8	4.2	—
Whittier and Wagner (1971)	58.8	4.9	—
Whittier and Wagner (1971)	56.4	4.7	—
Whittier and Wagner (1971)	50.2	3.0	—

[1] Collected by the author in New Jersey unless indicated otherwise.

Therefore, spore size in these plants was compared with that in *D. clintoniana* from northwestern New Jersey and *D. celsa* from Maryland. These data are presented in *Table 2*; data given by Whittier and Wagner (1971) were used for comparison. Two sizes of spores are evident, with the specimens from eastern New Jersey falling into the smaller size-class and comparable with *D. celsa* from Maryland and the data of Whittier and Wagner. The spores of *D. clintoniana* are larger, both in the specimens from northwestern New Jersey and as shown in the data of Whittier and Wagner. It appears, then, that the plants from Lodi and West Englewood, Bergen County, are *D. celsa*. Wagner (1971) also detected this genome in hybrids obtained in eastern New Jersey (*Table 1*). Unfortunately, most of the area where *D. celsa* apparently occurred has undergone rapid "development" in the last 25 years. The author has searched for populations of *D. celsa* in

Bergen County without success, including the areas from which the above material was collected. Wagner's material, collected by Gaede, was from an area destroyed by the construction of the Garden State Parkway.

Further confirmation that the material from northwestern New Jersey is *D. clintoniana* was obtained chemically by Widén and Britton (1971), to whom the author sent material collected from three populations in New Jersey. The results indicated close chemical similarity to *D. clintoniana* from other regions, although I had referred the material to Britton as *D. celsa* before chromosome counts were made from the New Jersey material.

This investigation shows that the large swampland *Dryopteris* from northwestern New Jersey (Morris, Passaic, Sussex, and Warren Counties) is *D. clintoniana*. Aside from cultivation in gardens, it is known from only these counties in New Jersey, always north of the glacial boundary and in the uplands. In New Jersey *D. celsa* occurred only in the Triassic Lowlands of Bergen County in the northeastern corner of the state, but it is now very rare or perhaps extinct there.

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Walter Sargeant Phillips (1905–1975)

CHARLES T. MASON, JR.*

After a lingering illness Walter Sargeant Phillips passed away on April 7, 1975, in the Santa Rosa Nursing Home in Tucson, Arizona.

Walter was born October 20, 1905, in Lynn, Massachusetts. At the age of five his family moved to Rochester, New York, where he spent his youth. During these early years his interest in photography was stimulated by the proximity to Eastman Kodak Company, and his curiosity about plants was promoted by his mother, who as an enthusiastic amateur taught him to use "Gray's Manual of Botany." He attended Kimball Union Academy in Meriden, New Hamsphire and obtained his baccalaureate degree from Oberlin College in Oberlin, Ohio. After graduation he became a part of the Oberlin program in China and was sent to the Ming Shen School in Taiku, Shansi, where he taught English from 1929 to 1931. As a person interested in traveling, this experience made a lasting impression.

On his return from China, he entered the University of Chicago, where he earned the Ph.D. in botany in 1935. With this degree he headed south to teach botany at the University of Miami in Florida. During the five years he spent in Florida he met Thelma Kinyoun, whom he married in 1940.

In September of the same year, they moved to Tucson where he joined the faculty of the University of Arizona as Assistant Professor of Botany. He steadily progressed through the professional ranks and became professor and head of the department in 1947. During the academic year 1954–55 he took his only sabbatical leave, having been awarded a Fulbright fellowship for study in Australia. In 1972, after thirty-two years of association with the University of Arizona, developing problems of health compelled him to accept emeritus status.

His love for young people was manifest in his work with the Boy Scouts and the joy he obtained from teaching. Although his training was in plant anatomy, which he taught during his tenure at Arizona, he worked for about ten years with the large beginning courses in botany and regretted that administrative duties forced him to turn those responsibilities over to others.

Walter enjoyed the unspoiled out-of-doors and for a time served as chairman of the Arizona Chapter of Nature Conservancy. Field trips and photography formed two of his principal hobbies. Each spring at the close of school, he, in the company of one or two other faculty members, would spend a week or more in the field in areas poorly known botanically, always in search of new sights and new plants, particularly ferns. It was his plan to write a book about Arizona ferns after retirement, a dream which never reached fruition. He belonged to several professional societies, including the American Fern Society for which he served as treasurer in 1958–1961. His publications include these pteridological papers:

1. Some notes on Arizona ferns. Amer. Fern J. **35:** 90–91. 1945.
2. Additional notes on Arizona ferns. Amer. Fern. J. **36:** 58–60. 1946.
3. Check-list of the ferns of Arizona. Amer. Fern. J. **36:** 97–108. 1946; **37:** 13–20, 39–51. 1947.
4. Psilotum nudum new to Arizona. Amer. Fern J. **60:** 30–32. 1970.

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Chromosome Numbers in the Genus Anogramma

GERALD J. GASTONY and JUDITH G. BAROUTSIS*,[1]

The genus *Anogramma* comprises six or seven species characterized by the annual habit of the sporophytes and the remarkable perennating mechanism of the gametophytes. Goebel's studies (1877, 1889, 1905) indicate that the gametophytes of *A. leptophylla* and *A. chaerophylla* are proterandrous and develop a positively geotropic growth, the "Fruchtsprosse" or archegoniophore, which eventually bears the archegonia. The distal end of this archegoniophore becomes a food storage tubercle which enables the gametophyte to survive environmental adversity. Goebel reports that upon resumption of favorable conditions, dormant embryos develop quickly by drawing on the reserve foods, or the tubercle gives rise to a new prothallial surface. All published reports of this perennation mechanism in *Anogramma* have apparently been based on Goebel's laboratory cultures of these two species alone. Nor have Goebel's observations been verified throughout the extensive ranges of these species, except for a brief comment by Mehra and Verma (1960) on Indian *A. leptophylla* and Proskauer's (1964) interesting observations on Australian material of the same species. In an effort to determine the universality of this perennating mechanism in *Anogramma*, a comparative study of gametophyte development in all available species is underway in our laboratory.

According to Tryon (1962), whose taxonomic treatment is followed here, these characters of annual sporophytes and perennial gametophytes in addition to differences in the rhizome scales and laminar indument distinguish the members of this genus from their closest relatives, the species of *Pityrogramma*.

In terms of species diversity, *Anogramma* is primarily a tropical to subtropical New World genus. *Anogramma chaerophylla* is widely distributed in tropical America, with collections known from Cuba, Hispaniola, Jamaica, Mexico, Brazil, Argentina, Uruguay, and Paraguay. This is the largest species, with fronds up to 20–30 cm long. *Anogramma guatemalensis*, questionably distinct from *A. leptophylla* at the species level, is known from Mexico to Costa Rica. *Anogramma Osteniana* is known only from Uruguay and Rio Grande do Sul, Brazil. *Anogramma Lorentzii*, the smallest species, with fronds up to 2–3 cm long, is known from Argentina, Uruguay, and Brazil. Lindman (1904) noted that a taxon he had previously (1903) described as *Gymnogramma Regnelliana* was better recognized as a variety of *Anogramma Lorentzii* (as *Gymnogramma Lorentzii* var. *megaspora*). This large-spored variety is known from Uruguay and Brazil, whereas the typical variety with smaller spores is presently known only from Argentina. *Anogramma leptophylla*, cited by Christ (1910) among the 13 species of cosmopolitan ferns, is known from Mexico and Central and South America, Europe, Asia, Africa, Australia, New Zealand, and islands adjacent to these

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areas. Two species of *Anogramma* do not occur in the Americas. *Anogramma ascensionis* is endemic to Ascension Island (34 square miles) in the south Atlantic Ocean. Its morphological affinities appear to be with *A. chaerophylla* (Hooker, 1854, as *Grammitis*; Goebel, 1889, as *Gymnogramma*). *Anogramma caespitosa* has recently been described from Mt. Kilimanjaro, Tanzania by Pichi Sermolli (1972).

As part of a biosystematic study of this genus, chromosome numbers are being determined for the several species and their various populations as these become accessible. The purpose of this communication is to report the new counts which have thus far been made and to appeal for help in obtaining additional viable materials of all species from the several areas of the world cited above.

MATERIALS AND METHODS

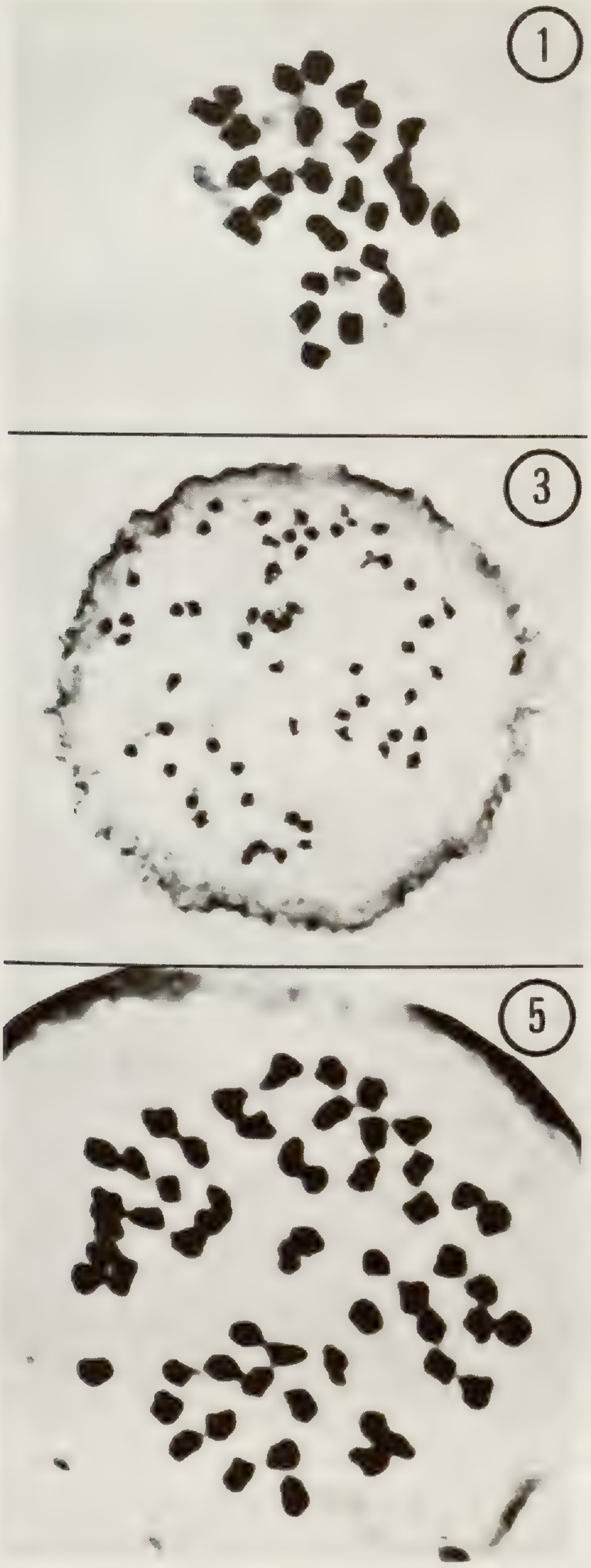
Meiotic counts were made from sporangia fixed for 12–24 hours in 3:1 absolute alcohol:acetic acid and then squashed and stained in acetocarmine (Manton, 1950). Slides were made permanent by the Sears (1941) method. Only a single chromosome squash is illustrated for each taxon, but three or more replicate counts of each have substantiated the illustrated numbers. Voucher specimens are deposited at the Indiana University herbarium (IND).

TABLE 1. CHROMOSOME NUMBERS IN ANOGRAMMA.

Number	*Voucher or Reference*	*Locality*	*Figures*
		Anogramma leptophylla	
n = 29	Brownlie (1958)	New Zealand	
ca. 56–57	Mehra and Verma (1960)	India	
ca. 58	Verma and Khullar (1965)	India	
26?	Tutin in Fabbri (1963)	U.K.: Jersey	
27 & 29	Mickel et al. (1966)	Mexico	
		Anogramma Osteniana	
29	A. Sehnem, 5 Nov 1972	Brazil: Rio Grande do Sul	1,2
		Anogramma Lorentzii var. megaspora	
58	A. Sehnem, 10 Oct 1972	Brazil: Rio Grande do Sul	3,4
		Anogramma chaerophylla	
29	Walker (1966)	Jamaica	
58	A. Sehnem, 12 Oct 1972	Brazil: Rio Grande do Sul	5,6

DISCUSSION

Table 1 lists all known chromosome counts reported for *Anogramma*. Mehra and Verma (1960) have proposed a generic base number of 29 based on Brownlie's count from New Zealand and their own counts of n=ca. 56–57 and n=ca. 56. They also reported an unequivocal count of n=58 and an approximate count of $2n$=116 in *Anogramma microphylla* to support the base number of 29 in the genus. As Tryon (1962) has shown, however, *A. microphylla* is appropriately excluded from this genus. Verma and Khullar (1965) subsequently confirmed the tetraploid nature of Indian *A. leptophylla* by their report of n=ca. 58. Mehra and Verma (1960) indicated that *Anogramma* is comparatively somewhat difficult cytological



FIGS. 1–6. Photographs and corresponding explanatory camera lucida tracings of the meiotic chromosomes of *Anogramma*. Collection data as in *Table 1*. FIGS. 1, 2. *A. Osteniana*, $n = 29$. FIGS. 3, 4. *A. Lorentzii* var. *megaspora*, $n = 58$. Interchromosomal thread-like processes presumably consist of matrical material. FIGS. 5, 6. *A. chaerophylla*, $n = 58$.

material; we can confirm this observation. This difficulty apparently accounts for the approximate counts given by Mehra and Verma (1960) and by Verma and Khullar (1965) and for the questionable count of $n=26$ made by Tutin (in Fabbri, 1963). If the count of $n=27$ for Mexican *A. leptophylla* given by Mickel et al. (1966) is not an artifact of the difficult nature of cytological material in this genus, it is the only aneuploid count known thus far in *Anogramma*.

Our new counts listed in *Table 1* agree with the generic base number of 29 suggested above. *Anogramma Osteniana* has now been counted for the first time and is clearly at the diploid level. In addition to the polyploidy previously reported for *A. leptophylla (Table 1)*, *A. chaerophylla* is now also known at the diploid and tetraploid levels, with $n=29$ reported from Jamaica (Walker, 1966) and $n=58$ here reported from Brazil.

The count of $n=58$ for Brazilian *A. Lorentzii (Table 1)* is significant in view of the infraspecific taxonomy proposed by Lindman (1904). The size range of 10 randomly sampled dry spores from our Brazilian material is 66–79μm in equatorial diameter, clearly indicating its affinity with Lindman's (1904) large-spored variety. Thus the well-known relationship between spore size and ploidy level (Tryon, 1968; Whittier & Wagner, 1971) is probably borne out here. Our data suggest a polyploid series in this species, with the large-spored variety a tetraploid and the smaller-spored Argentine variety representing the diploid level. Unfortunately, Argentine material has not yet been available for counting.

In order to further this work, living sporophytes or air-dried (not over heat) vouchers with viable spores are requested from correspondents in all parts of the world. Material of all species is solicited, but there is special need of specimens of *A. ascensionis*, *A. caespitosa*, and *A. Lorentzii* var. *Lorentzii* from Argentina.

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REVIEW

"NUMERICAL TAXONOMIC STUDIES ON NORTH AMERICA LADY FERNS AND THEIR ALLIES," by Fah-Seong Liew, Taiwania **17:** 190–221. 1972.—Dr. Liew has done a comprehensive numerical taxonomic study of the Lady Ferns of temperate North America and, to a lesser extent, of northern Europe. Ninety-three characters of the mature sporophytes, mostly from the fronds, were analyzed, plus geographic range and five spore characters. Complex and apparently taxonomically sound taxiometric methods were used to classify the taxa phenetically. In addition, a ground plan diagram was constructed using 14 characters of the mature sporophytes and three of the spores.

The results of Liew's analysis are of interest because of the longstanding disagreements among taxonomists concerning the classification of the Lady Ferns. According to Liew, there are three groups: (1) *Athyrium thelypterioides* (Michx.) Desv. and *A. pycnocarpon* (Spreng.) Tidestr. are North American. (2) *Athyrium distentifolium* Tausch ex Opiz is divided into subsp. *distentifolium* from eastern Asia and subsp. *americanum* (Butters) Liew from Alaska, Canada, and the northwestern United States. This species seems to have evolved from *A. filix-femina*. The combination proposed by Liew has not yet been validly published; until that time, the taxon must be known as var. *americanum* (Butters) Boivin. (3) *Athyrium filix-femina* is divided into four subspecies. Subspecies *angustum* (Willd.) Clausen is from northeastern North America, and subsp. *asplenioides* (Michx.) Hultén is from the southeastern United States. These subspecies are closely related phenetically and phylogenetically. Liew attributes both of these combinations to himself, incorrectly. Subspecies *filix-femina* from Europe and subsp. *cyclosorum* (Rupr.) C. Chr. from the northwestern and the southwestern United States are more closely related to each other than they are to the eastern North American subspecies. The northwestern and southwestern United States forms of subsp. *cyclosorum* can be separated only by characters of spore sculpture, and so do not merit separate taxonomic recognition. The taxiometric analysis agrees, as Liew says, "reasonably well with groups drawn by close observation both in the field and in the herbarium."—*D.B.L.*

Selaginella ludoviciana, S. apoda and Their Hybrids in the Southeastern United States

PAUL SOMERS* and WILLIAM R. BUCK**,[1]

The Gulf Spike-moss, *Selaginella ludoviciana* A. Braun, has been synonymized with the Meadow Spike-moss, *Selaginella apoda* (L.) Spring, by numerous authors in recent years (Brown & Correll, 1942; Correll, 1956; Lundell, 1966; Ward, 1968; Correll & Johnston, 1970). Our investigations, however, indicate that significant morphological and anatomical differences do exist between the two. *Selaginella ludoviciana* may be easily recognized by its assurgent, stiff branches and by microphylls with hyaline borders, which are 3–5 cells wide and often visible without magnification (*Fig. 6*). *Selaginella apoda*, on the other hand, is usually prostrate and has either undifferentiated or only slightly hyaline leaf margins (*Fig. 1*).

More subtle differences between the two species were revealed by anatomical studies of stems and leaves (Buck, 1974) and by examination of spores with the light microscope and the scanning electron microscope. For instance, in *S. ludoviciana* stomata are restricted to a few rows adjacent to the midribs of the leaves (*Fig. 5*), whereas in *S. apoda* they are scattered throughout the laminae (*Fig. 2*). Also, examination of leaf clearings and scanning electron micrographs showed a high percentage of papillate cells scattered throughout the lower epidermis of *S. ludoviciana* leaves and very few, if any, on those of *S. apoda* (*Figs. 2* and *5*).

Comparisons of the spores of the two species reveal other differences. Knox (1950) described the microspores of both species as being warty with crenate margins. Hieronymus (1900), however, distinguished the species by their microspore morphology, describing those of *S. ludoviciana* as smooth and those of *S. apoda* as warty, verrucose, or irregularly rugose. In our study, we consistently found the microspores of *S. ludoviciana* to be smooth and those of *S. apoda* to be warty when viewed with the light microscope, thus confirming Hieronymus' findings. When viewed with the SEM, the microspores of *S. apoda* can be described as rugulo-reticulate (*Figs. 8* and *9*) to verrucate. Terminology for these spore wall descriptions is based primarily on that defined by Harris (1955). In some specimens (*Fig. 7*) the spores of *S. apoda* are covered with small spicules or papillae. In *S. ludoviciana* the so-called smooth spores are in fact covered with short papillae or spicules (*Figs. 10–12*). Measurements of microspores from 16 specimens of each species failed to show a significant size difference ($\bar{x} = 26.47\mu m$ for *S. apoda* and $\bar{x} = 27.24\mu m$ for *S. ludoviciana*).

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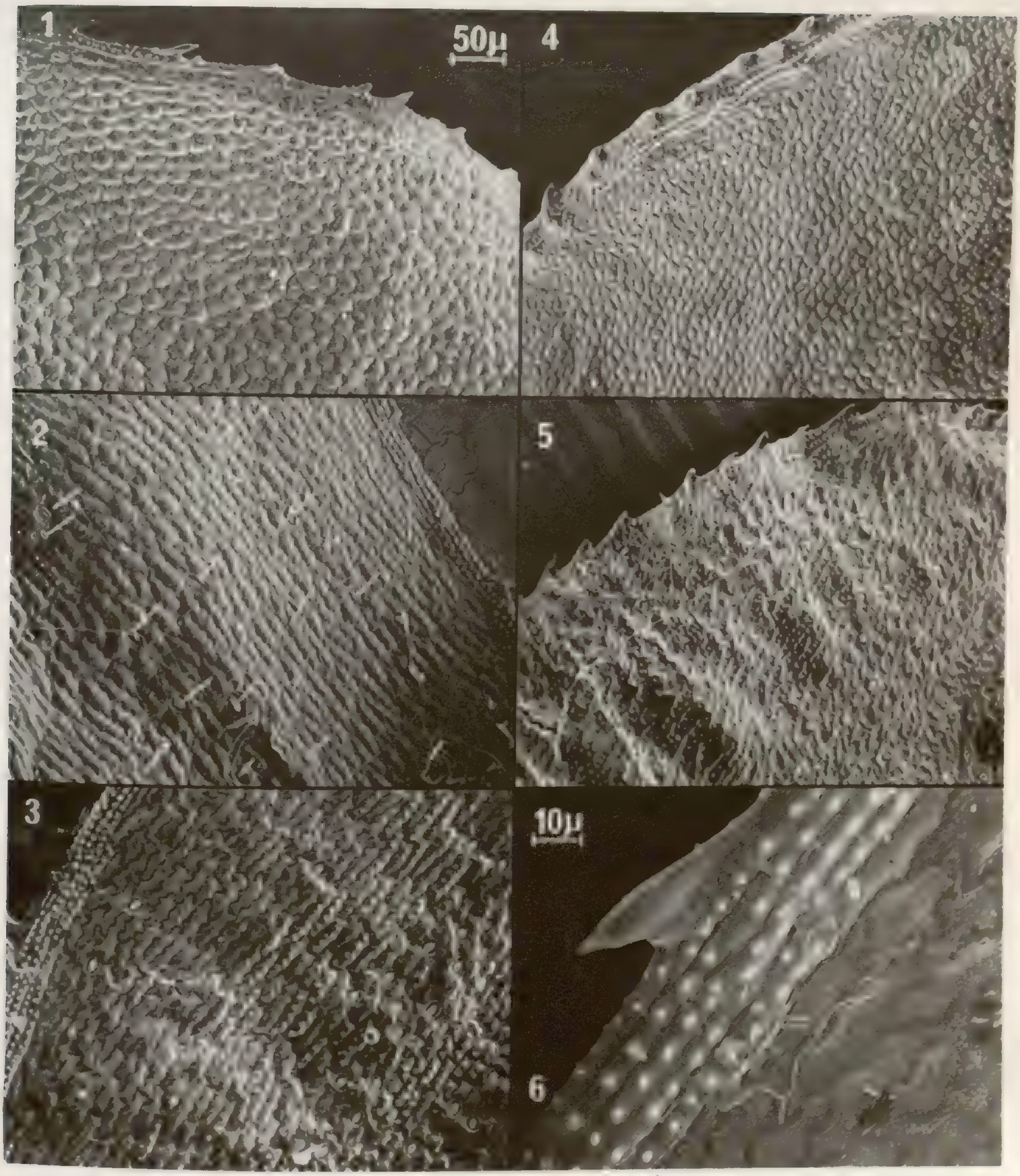
[1]We wish to thank the curators of the following herbaria for the loans which made this study possible: ALU, DUKE, FLAS, FSU, GA, GH, LAF, LSU, MICH, MISSA, MO, NCSC, NCU, NO, NY, OKL, OKLA, SMS, TENN, TEX, UARK, UMO, US, USF, VDB, VSC, and the Herbarium of the University of Mississippi. The senior author wishes to thank the Department of Chemical & Metallurgical Engineering, University of Tennessee for use of their AMR Model 900 SEM.

Contribution from the Botanical Laboratory, the University of Tennessee, N. Ser. No. 448.



Selaginella leaves. FIGS. 1–2. *S. apoda*, Horry Co., So. Car., 8 July 1945, *Coker* (NCU). FIG. 1. Upper epidermis. FIG. 2. Lower epidermis with stomata indicated by arrows. FIG. 3. Presumed hybrid, *S. apoda* × *ludoviciana*, lower epidermis, Levy Co., Fla., *Kral & Kral 6960* (GA). FIGS. 4–6. *S. ludoviciana*, Liberty Co., Fla., *Godfrey 72961* (TENN). FIG. 4. Upper epidermis. FIG. 5. Lower epidermis. FIG. 6. Differentiated cells of hyaline margin, lower epidermis.

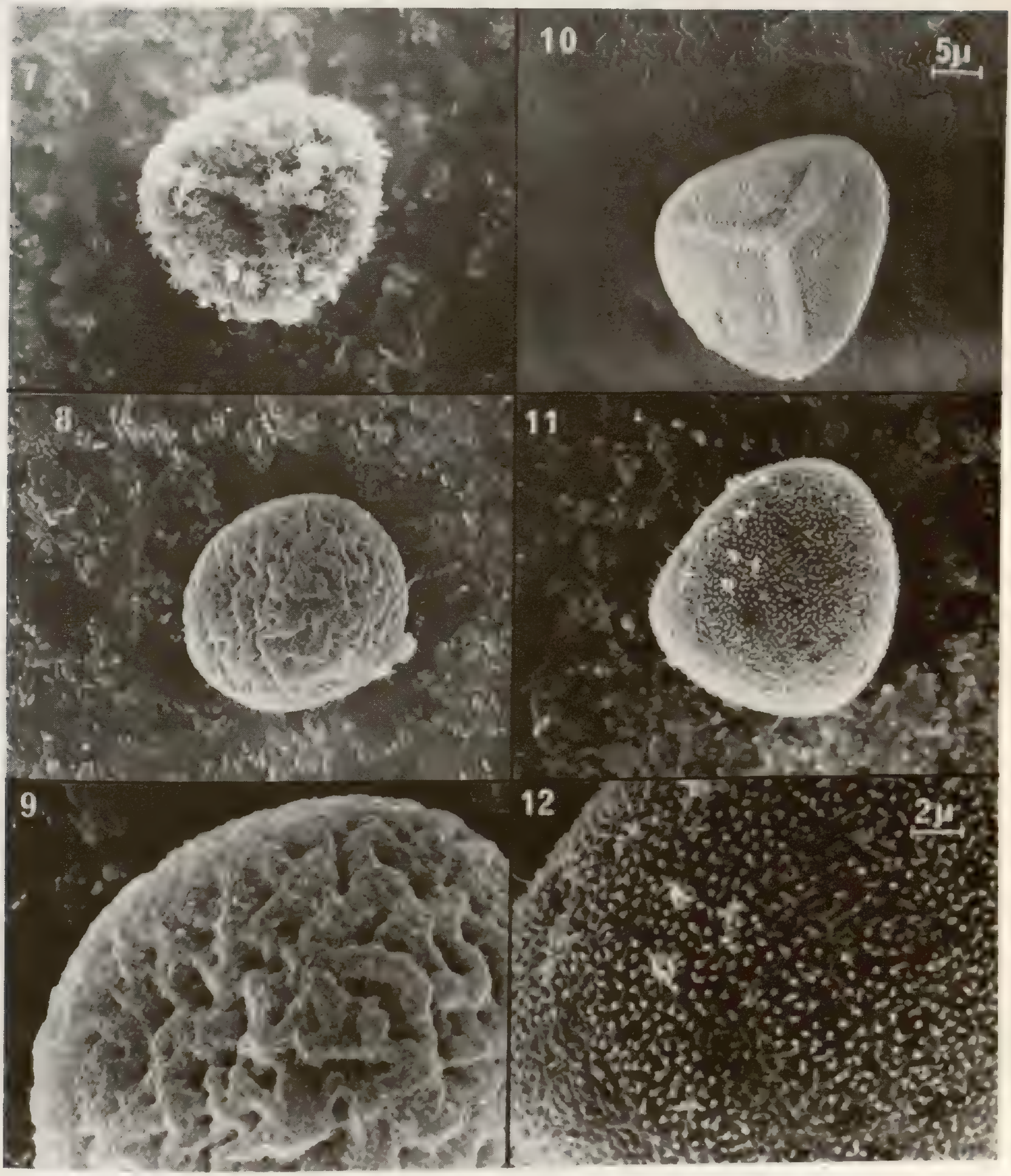
Megaspore morphology of the two species is quite similar (*Figs. 13* and *15*), but the muri (ridges) appear lower and the equatorial ridges less prominent in *S. ludoviciana (Fig. 15).* Variation in the fine structure of the areolae and muri exists (*Figs. 14* and *16*), but there is probably as much variation within *S. apoda* as there is between the two species. Megaspores of *S. ludoviciana* are demonstrably larger than those of *S. apoda*. Measurements of spores from 13 specimens of *S. apoda* and 9 specimens of *S. ludoviciana* showed a significant difference in the means at the 97.5% confidence level with the Mann-Whitney U-test, ($\bar{x} = 451\mu m \pm 53$ for *S. ludoviciana* and $\bar{x} = 359\mu m \pm 23$ for *S. apoda*). These measurements were made within 24 hrs. after the spores were mounted in Hoyer's medium. Measurements from slides one year old yielded mean values around 70μm higher than those from fresh preparations.

The distribution of *S. ludoviciana (Fig. 19)* extends from the northeast coast of Florida to the southeast corner of Louisiana. Small (1938) reports it from Texas, and Cory and Parks (1937) state that it grows in the Timber Belt and Coastal Prairies of Texas. Our survey of many herbaria, however, fails to document these reports. Supposedly the Cory and Parks' vouchers are in the Tracy Herbarium, but according to Dr. Frank Gould, no *S. ludoviciana* specimens are deposited there. For these reasons we consider the western limit to be in St. Tammany and Orleans Parishes, Louisiana, and Hinds County, Mississippi. The only available flora of Mississippi (Lowe, 1921) and a recent pteridophyte checklist of Mississippi (Jones, Pullen & Watson, 1969) report only *S. apoda* in the state. We find, however, that *S. ludoviciana* occurs in five southern Mississippi counties. For Alabama, we can cite only one collection, from Baldwin County, but Mohr (1901, p. 322) reports its occurrence in the pine barrens of Mobile County. Although Thorne (1954) treats the two taxa as a single species, he indicates the presence of both *S. apoda* and *S. ludoviciana* in southwestern Georgia, as indicated on our map.

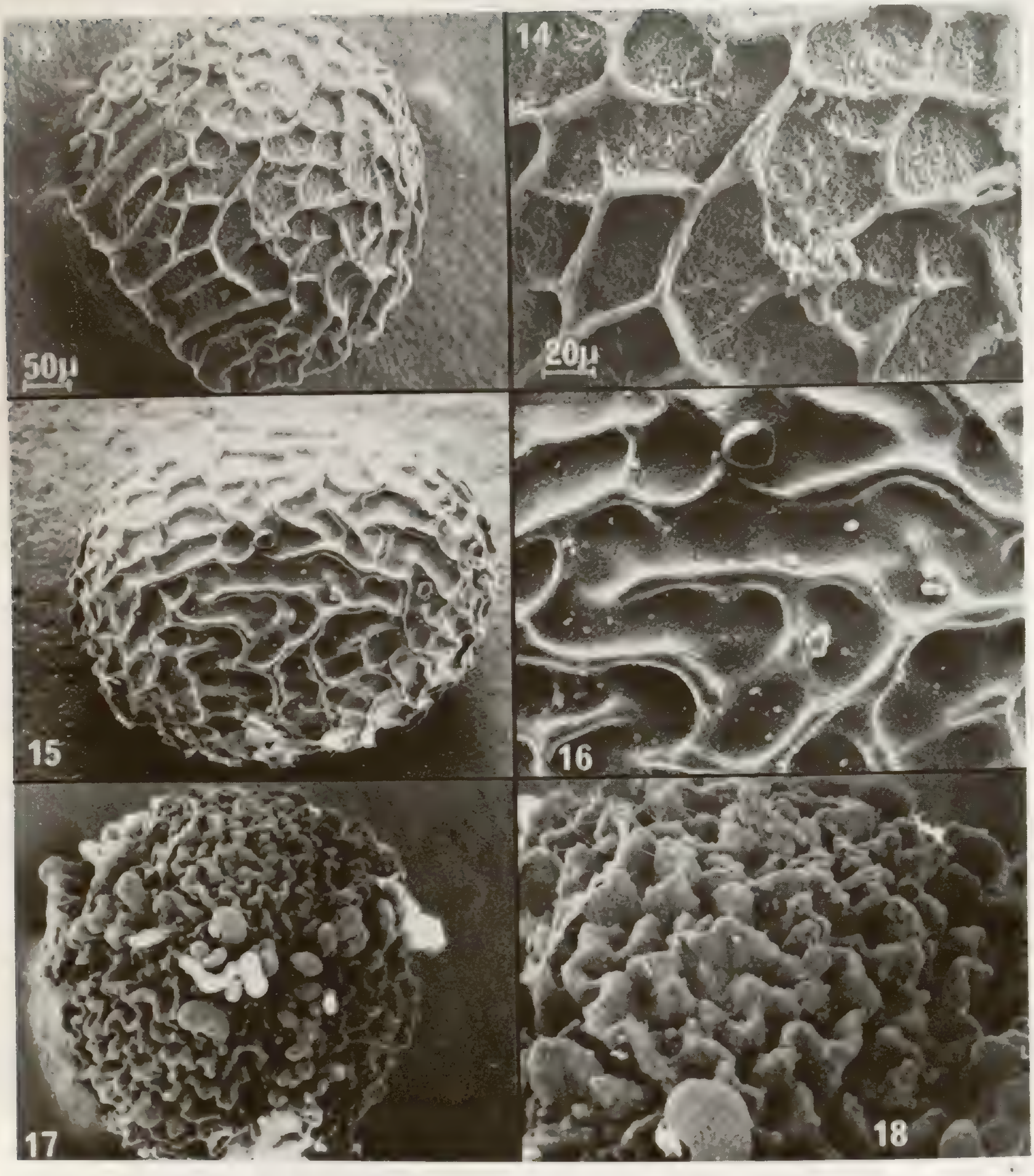
The habitats of *S. ludoviciana* include shaded to open woods, calcareous ledges and knolls, and rich, wooded ravines. Usually the sites are described as wet: springs, swamps, banks of streams, ditch banks or moist ravines. Population size varies. Along exposed streams and ditches the plants may form dense mats several meters across with the ascending branches up to 10–15 cm high. In more shaded and drier habitats of wooded areas the colonies usually consist of only a few individuals.

Selaginella apoda has been found in all of the gulf coast states, but it appears to be more frequent in the Appalachian and Cumberland mountains and in the Piedmont than on the Coastal Plain itself. Actually there is very little overlap in the ranges of the two species. The only areas where both species have been collected are St. Tammany Parish, Louisiana; Stone County, Mississippi; the Apalachicola River area in Florida, and Duval County, Florida.

Since the two species seldom occur in close proximity and mechanisms of long distance spore dispersal are nearly absent in *Selaginella*, hybrids between them are probably rare. Two collections, however, show evidence of possible hybrid origin: *Arsène 11648*, and *Kral & Kral 6960*. Although the Arsène collections at



Selaginella microspores. FIG. 7. *S. apoda*, proximal view, Tangipahoa Parish, La., *Thieret 19655* (FSU). FIGS. 8–9. *S. apoda*, distal views, Bledsoe Co., Tenn., *Sharp, Shanks & Clebsch 3489* (TENN). FIG. 10. *S. ludoviciana*, proximal view, Liberty Co., Fla., *Godfrey 72961* (TENN). FIGS. 11–12. *S. ludoviciana*, distal views, George Co., Miss., *Pullen 63137* (GA).



Selaginella megaspores. FIGS. 13–14. *S. apoda*, lateral views, Gilmer Co., Ga., *Duncan 22125* (GA). FIGS. 15–16. *S. ludoviciana*, distal views with microspore on surface, Liberty–Gadsden Co. line, Fla., *Wagner, Godfrey & Mitchell 62036* (TENN). FIGS. 17–18. Presumed hybrid *S. apoda* × *ludoviciana*, distal views, St. Tammany Parish, La., *Arsène 11648* (LSU).

LSU and US have slightly different locality data, they are presumed duplicates. Megasporangia from the Arsène collection have only one megaspore, instead of four. In addition, the spore wall structure is atypical (*Figs. 17* and *18*). The size of the megaspores varies, but most appear to be exceptionally large. In the Kral collection the megasporangia observed had four, apparently normal megaspores.

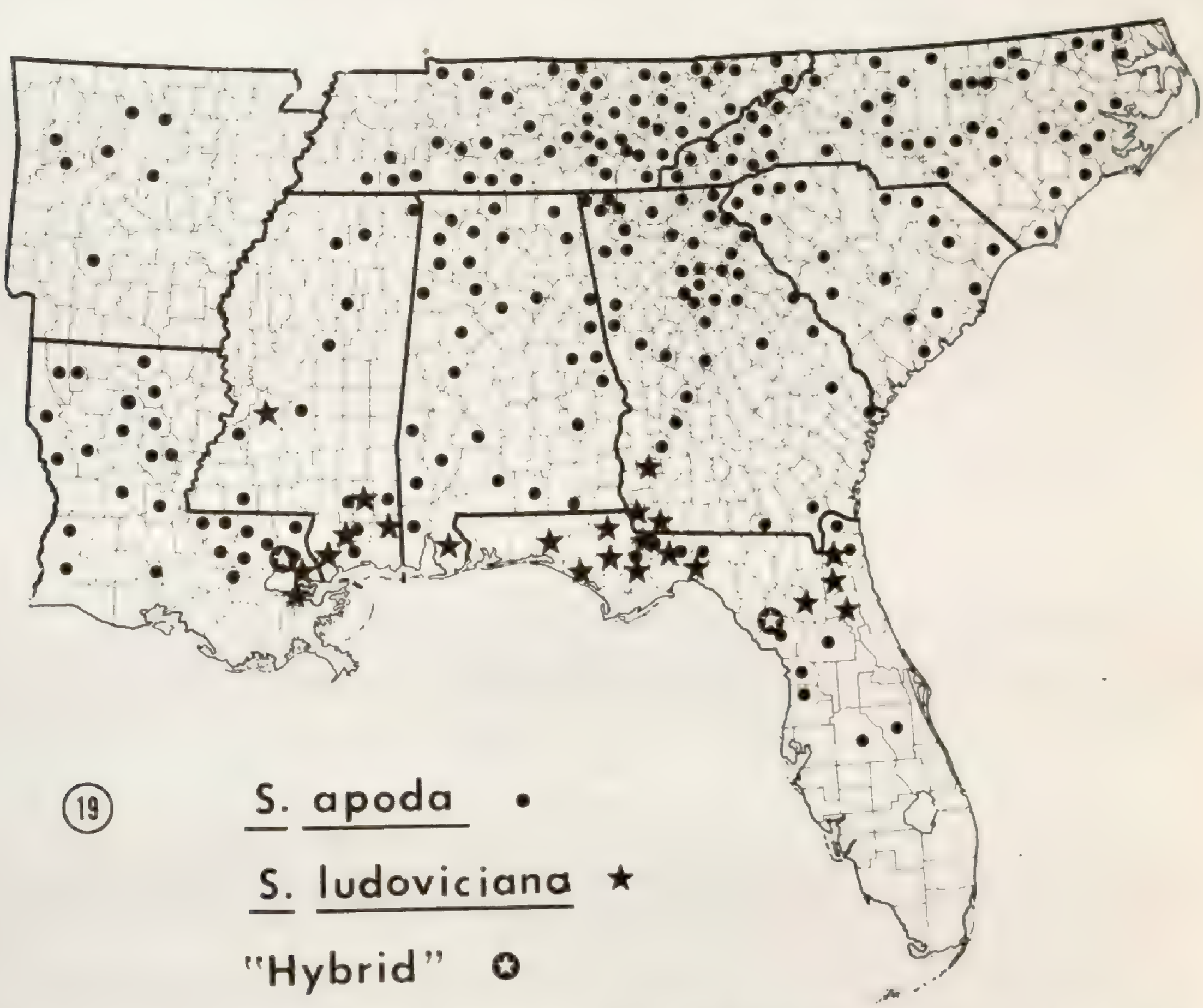


FIG. 19. Distribution of *Selaginella apoda*, *S. ludoviciana*, and two presumed hybrids in the southeastern United States.

The microspores of both collections are highly variable in size and structure. In the Arsène collection most of them are small and misshapen, and apparently abortive. A few are larger than normal and lack the typical trilete scar. The Kral collection also has a high frequency of aborted microspores and displays variability in the microspore wall patterns. The leaves of both collections are intermediate in several respects, with 3 or 4 rows of marginal hyaline cells and a lower epidermis with many papillate cells (*ludoviciana* characteristics), but have stomata throughout the lamina (an *apoda* characteristic, *Fig. 3*). Both collections are presumed to be of hybrid origin.

Because *S. apoda* is a distinctive and widespread species, localities have not been cited below.

SPECIMENS OF S. APODA × LUDOVICIANA EXAMINED:

LOUISIANA: St. Tammany Parish: Covington: S. Paul (LSU) or Covington: Sulphur Springs (US), *Arsène 11648* (LSU, US).

FLORIDA: Levy Co: 0.5 mi S of Gulf Hammock on peaty stream bank, *R. & M. Kral 6960* (FLAS, FSU, GA, USF).

REPRESENTATIVE SPECIMENS OF S. LUDOVICIANA EXAMINED:

FLORIDA: Alachua Co.: Gainesville, 15 April 1972, *Griffin* (TENN); **Bay Co.:** Moccasin Creek N of Bennett, *McDaniel 7256* (FSU); **Calhoun Co.:** 7 miles S of Altha, *Godfrey 62717* (FSU, NCU); **Clay Co.:** Bluff of Black Creek, near Middleburg, *Diddell 148* (FLAS): **Duval Co.:** Near Jacksonville, *Curtiss 3799* (FLAS); **Gadsden Co.:** Apalachicola River at Aspalaga, W of Greensboro, *Godfrey 52905* (NCSC); **Jackson Co.:** Grand Ridge, *Palmer 35268* (MO); **Jefferson Co.:** Monticello, 15 March 1891, *Lighthipe* (MICH); **Leon Co.:** Near Ochlocknee River, W of Tallahassee, *Godfrey 52951* (FSU, GA, NCU, USF, VDB); **Liberty Co.:** Rock bluff along Apalachicola River, *Correll & Kurz 5675* (DUKE, US); **Putnam Co.:** Valley of Cabbage Creek, 4 miles S of Interlachen, *Ward & Myint 2312* (FLAS); **Walton Co.:** About 11 miles S of De Funiak Springs, *Ward 6580* (FLAS).

GEORGIA: Calhoun Co.: Ichawaynochaway Creek, 3 miles W of Leary, *Thorne & Muenscher 8035* (GA); **Decatur Co.:** 1 mile N of River Junction, *Pyron & McVaugh 2245* (GA, US); **Seminole Co.:** Chattahoochee River at Butler Landing, *Thorne & Muenscher 2312* (GA, US).

ALABAMA: Baldwin Co.: Magnolia Springs, 30 August 1953, *White* (ALU).

MISSISSIPPI: George Co.: White Bluff area of University of Mississippi forest lands, *Pullen 63137* (GA, NCU, Univ. Miss.); **Hancock Co.:** About 1 mile N of Logtown, *Diener 1438* (MISSA); **Hinds Co.:** Baldwin Farris Plantation, 1860, without collector, (MICH); **Perry Co.:** W of Leaf, sec. 21, T.1N., R.9W., *Jones 11006* (Univ. Miss.); **Stone Co.:** S of Perkinston, on U. S. Forest Service Hiking Trail, *Jones 4968* (Univ. Miss.).

LOUISIANA: Orleans Parish: North New Orleans, *Pinkerton 148* (MO); **St. Tammany Parish:** Between Mandeville and Madisonville, *Ewan 17883* (NO).

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The Origin of the Apical Cell in Psilotum Gametophytes

DEAN P. WHITTIER*,[1]

Three investigators have germinated *Psilotum* spores. Darnell-Smith (1917) and Bierhorst (1955) accomplished germination by mixing the spores in soil, whereas Whittier (1974) germinated the spores on a nutrient medium in axenic culture. Bierhorst (1955) recovered gametophytes in one- and two-celled stages after 15 months and a more complex gametophyte after 26 months. However, he found no stages that could be used for comparison with Darnell-Smith's report of the later stages of germination and the origin of the apical cell. Whittier reported some early stages of germination and gametophyte development that did not agree with Darnell-Smith's description of apical cell origin. Consequently, more stages of germination and early gametophyte development from axenic culture have been studied to determine how the apical cell of *Psilotum* gametophytes is formed.

MATERIALS AND METHODS

The source of the spores of *Psilotum nudum* (L.) Beauv. and the axenic culture techniques were those of Whittier (1974). The spores were sown and placed in the dark to germinate. After six or more months in the dark, young gametophytes were collected from the cultures. Gametophytes in various stages of development were cleared and stained with acetocarmine–chloral hydrate, according to Edwards and Miller (1972). This technique makes the cell walls easily observable by removing the starch and clearing the plastids; it also stains the nuclei red. The cleared and stained gametophytes were photographed, and the photographs were traced to provide the illustrations for the present report. Since *Psilotum* gametophytes attain three-dimensional growth early in their development, in most cases cells and/or nuclei of cells lying behind other cells are denoted with dashed lines in the illustrations.

OBSERVATIONS

The bean-shaped, monolete *Psilotum* spores, as shed from the sporangium, contain a single, uninucleate cell (*Fig. 1*). In the first stage of germination, the spore coat or wall ruptures along the monolete aperture and the cell within bulges out (*Figs. 2* and *3*). After this, a wall perpendicular to the polar axis of the spore divides the original cell into a proximal cell that protrudes outside the spore coat and a distal cell that remains inside the spore coat (*Fig. 4*).

The distal cell usually remains within the spore coat for a short time. Occasionally the distal cell divides to form two cells (*Figs. 6* and *10*). One young gametophyte was found with three cells derived from the distal cell. The cells derived from the distal cell have never been observed to contribute to the formation of the apex of the gametophyte.

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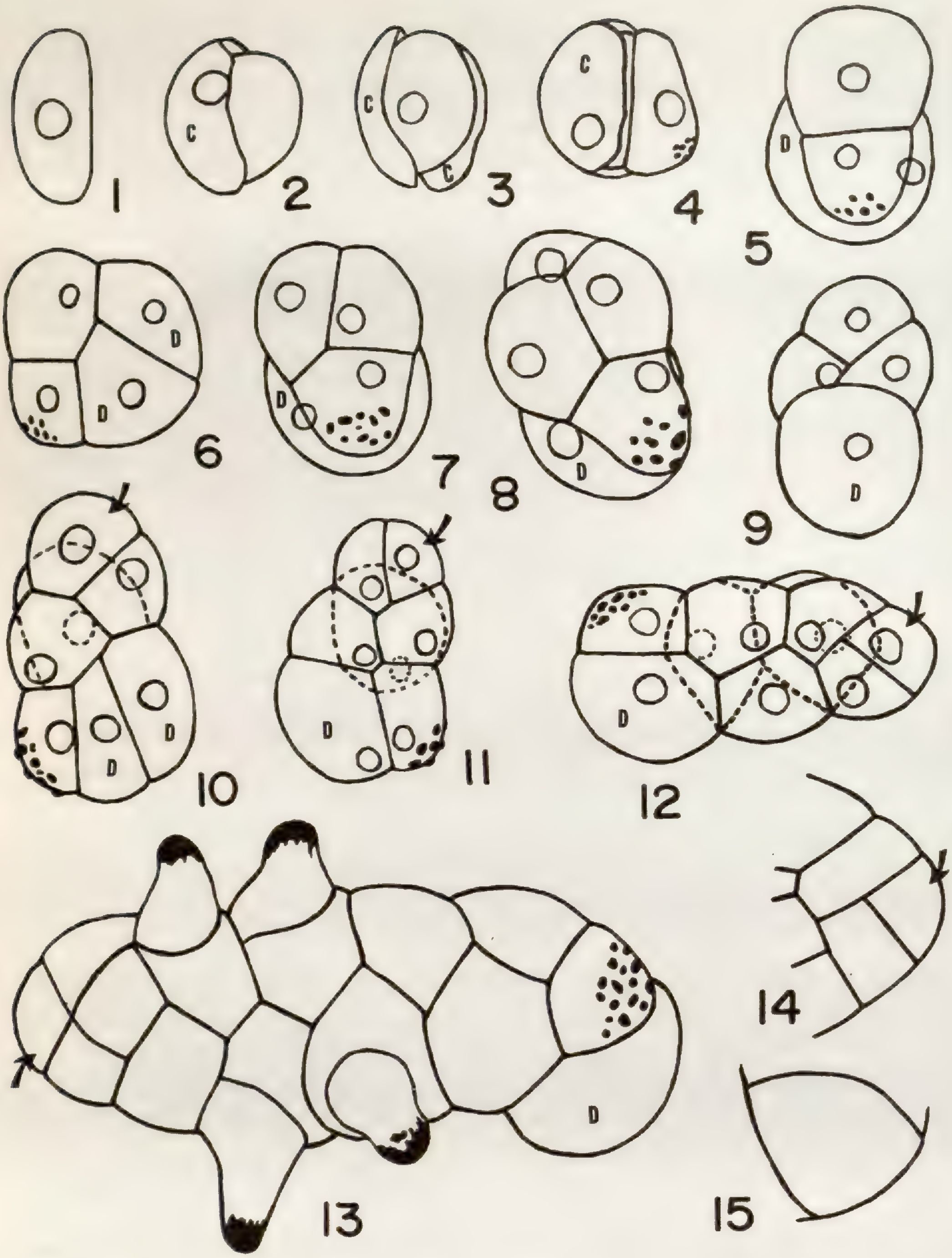
[1] I want to thank Dr. James L. Riopel, of the University of Virginia, for supplying the spores used for this study and the Vanderbilt University Research Council for support of this research.



Psilotum spore germination and gametophyte development. FIGS. 1–12, ×350; C = spore coat or wall, D = distal cell or products of distal cell, and arrow = apical cell of the gametophyte. FIG. 1. Uninucleate spore. FIG. 2. Germinating spore with a single cell, side view. FIG. 3. Same, proximal view. FIG. 4. Two-celled gametophyte with proximal cell protruding outside spore coat and distal cell still inside spore coat. FIG. 5. Three-celled gametophyte in proximal view, showing apical and basal (spotted) derivatives of proximal cell. FIG. 6. Four-celled gametophyte in side view with two cells

The proximal cell gives rise to the gametophyte's apex. It is asymmetrical, with one end larger than the other (*Fig. 4*). The larger, basal end has brown spots that are an excellent marker for identifying cells in the later stages of gametophyte growth. The proximal cell divides perpendicular to its long axis and forms two cells (*Figs. 5* and *6*). The cell with brown spots, which was derived from the basal end of the proximal cell, has never been observed to undergo cell division. The brown spots on some gametophytes appear as wall protuberances (*Figs. 10* and *11*). The derivative of the apical end of the proximal cell enlarges and divides obliquely (*Fig. 7*). Enlargement of the smaller of the two cells thus produced is followed by a division almost perpendicular to the oblique cell wall (*Fig. 9*). These two divisions form three cells from the apical derivative of the proximal cell (*Figs. 8* and *9*). The smallest cell produced by the second division enlarges and undergoes a division which gives rise to the apical cell of the gametophyte and another cell (*Fig. 10*). Thus, a domed apical cell of the gametophyte with three cutting faces appears after three divisions have occurred in the apical derivative of the proximal cell (*Fig. 10*). *Figures 11* and *12* illustrate that the divisions of the apical cell cut off cells which contribute to the growth of the gametophyte and maintain the three cutting faces of the apical cell. As the gametophyte becomes somewhat older, the apical cell retains its tetrahedral shape and three cutting faces, but becomes somewhat less domed (*Figs. 13–15*). In addition, the derivatives of the apical cell, which remain undivided in the younger gametophytes (*Figs. 11* and *12*), divide to form rhizoids with brown tips (*Figs. 13*).

DISCUSSION AND CONCLUSIONS

Germination up to the two-celled stage is the same as was described by Darnell-Smith (1917). However, his description of the later stages of germination and apical cell formation do not agree with what has been observed in the present study.

Darnell-Smith claimed that the cell with yellowish-brown patches (or brown spots) became the apical cell. Also, he thought the yellowish-brown patches were chromoplasts. But this is unlikely for two reasons: chloral hydrate treatment would have rendered the chromoplasts colorless, which did not occur, and the brown spots often are protuberances of the cell wall (*Figs. 10* and *11*) and have the same color as rhizoid tips on older gametophytes (*Fig. 13*). It appears from this evidence that the brown spots or yellowish-brown patches are part of the cell wall, and are not cytoplasmic structures. Contrary to Darnell-Smith's description, the brown spots do not fade. Thus, even on older gametophytes the cell formed from

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from proximal cells as in FIG. 5 and two cells from distal cell. FIG. 7. Gametophyte with three cells from proximal cell. FIG. 8. Gametophyte with three cells from apical derivative of proximal cell. FIG. 9. Same, viewed from opposite side to show second cell wall formed in apical derivative of proximal cell. FIG. 10. Gametophyte with four cells from apical derivative of proximal cell, including apical cell of gametophyte. FIG. 11. Gametophyte after apical cell has divided one time. FIG. 12. Gametophyte after apical cell has divided three times. FIG. 13. Older gametophyte showing apical cell, spotted basal derivative of proximal cell, and rhizoids tipped with similar colored material as spotted cell, ×400. FIG. 14. Section through apex of older gametophyte showing apical cell, ×320. FIG. 15. Surface view of apical cell of older gametophyte, ×400.

the basal end of the proximal cell can be identified at the basal end of the gametophyte (*Fig. 13*). Since the coloration of the wall material on the brown-spotted cell and the tips of the rhizoids is the same, it is possible that the brown-spotted cell is an abortive rhizoid.

The brown-spotted cell does not become the apical cell of the *Psilotum* gametophyte, for it would have to divide, which it does not appear to do. Also, the brown-spotted cell is essentially unchanged (with the exception of enlargement) from the time it is formed to the time it can be observed on gametophytes with functional apical cells (*Figs. 10–13*).

Holloway (1939) reported that the apical cell of sexually mature gametophytes varies in size and shape and has four cutting faces. The tetrahedral apical cell with three cutting faces *(Figs. 10-15)* is not a stable feature of *Psilotum* gametophytes as they become older and sexually mature. However, Bierhorst (1953) concluded that the apical cell with three cutting faces is characteristic of the gametophyte and that any apparent deviations from this shape are due to the enlargement and variations in the shape of the most recent derivatives of the apical cell.

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Stem Anatomy and Phyllotaxis in Ophioglossum petiolatum

EMILY WEBB*,[1]

Besides *Ophioglossum petiolatum* Hooker, subg. *Ophioglossum* includes approximately 20 other species. All are characterized by a radially erect, underground stem which bears a simple, oval or lanceolate leaf blade at the base of which arises a sporangia-bearing segment (Campbell, 1911, p. 86; Claussen, 1938, pp. 111–112, 1954). Stem anatomy of only seven species has been described: *O. vulgatum* (Rostowzew, 1891; Vasisht, 1927), *O. moluccanum* (Campbell, 1911), *O. aitchisonii* (Vasisht, 1927), *O. fibrosum* (Maheshwari & Singh, 1934), *O. littorale* (Nozu, 1956), *O. lusitanicum* (Gewirtz & Fahn, 1960), and *O. reticulatum* (Sen, 1968).

At the base of the stem is a protostele surrounded either partially or completely by phloem. Above this point pith develops, and the stele is an ectophloic siphonostele. The remainder of the stem contains a dictyostele of anastomosing collateral bundles with endarch xylem and no secondary vascular tissues. Root bundles are attached at the meristele edges. It is not known whether roots are associated consistently with leaf bases. Rostowzew found one root attached near each leaf base in *O. vulgatum*, and Vasisht found the same condition in *O. aitchisonii*. It seems possible that the roots of some species bear no discernible relation to the leaf bases; figure 2 of Gewirtz and Fahn may be interpreted as indicating this.

Leaf gaps are spirally arranged up the stem; this may reflect phyllotaxis, but whether this is so is not clear from descriptions that have been published.

It is desirable to describe the stem anatomy of additional species of subg. *Ophioglossum* in detail because if stem architecture is better known in more species, it may be of value in establishing phylogenetic lines within the subgenus. Since the origin of subg. *Ophioglossum* is unknown and because it is considered the most primitive of the subgenera (Nishida, 1952; Claussen, 1954), clues to the origin of *Ophioglossum* might be found by comparing its stem anatomy with that of fossil stems possibly related to *Ophioglossum*. Many authors have discussed the origin of *Ophioglossum*, among them Eggert (1964), Bower (1908, p. 493, 1935, pp. 459, 463, 472, 604), and Bierhorst (1971, p. 151). Several species of subg. *Ophioglossum* may be conspecific, including *O. petiolatum*, *O. littorale*, and *O. moluccanum* (Claussen, 1938, pp. 134, 136). Stem anatomy comparisons of these species may be useful in determining their relationship.

This report presents an anatomical study of representative stems of *O. petiolatum* in which leaf and root gap patterns in the xylem are delineated and the relation of roots to gaps and to leaf bases is examined.

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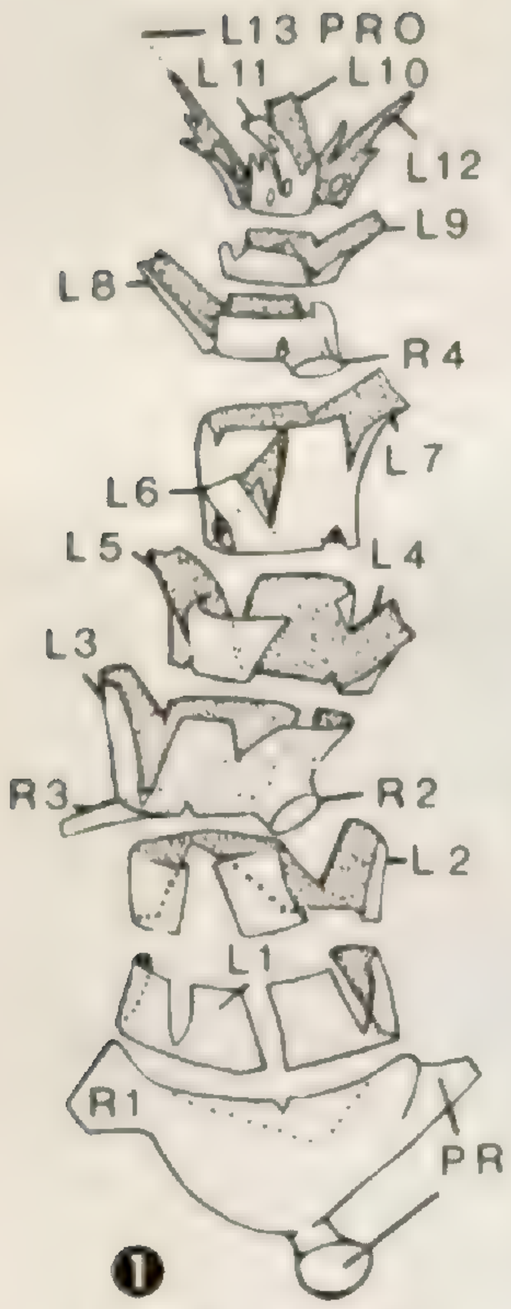

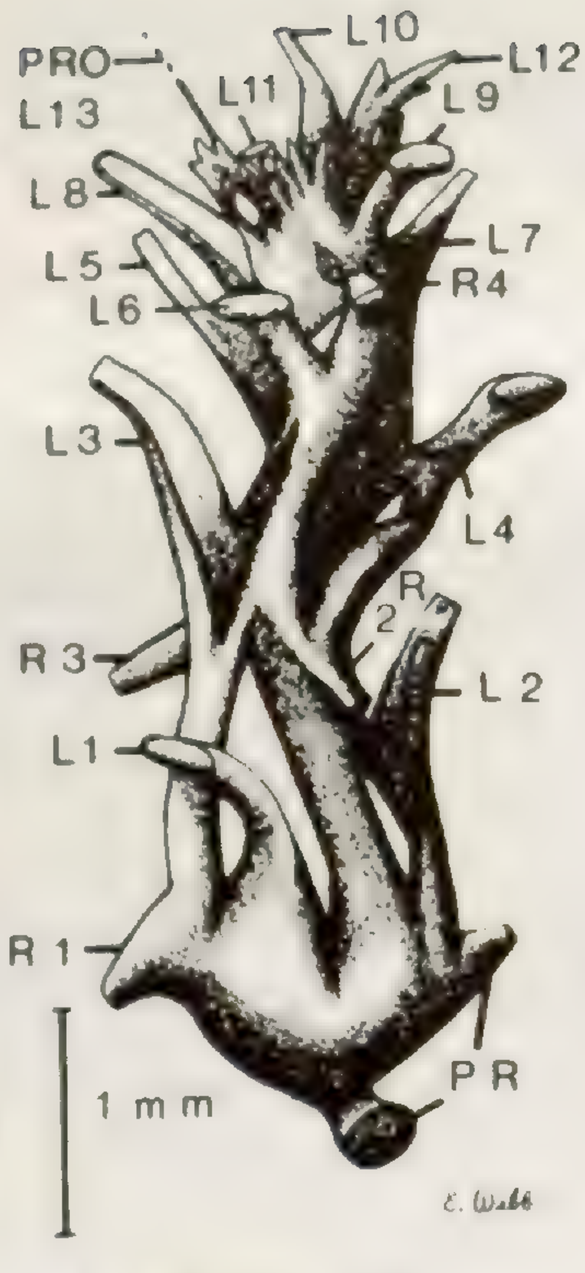

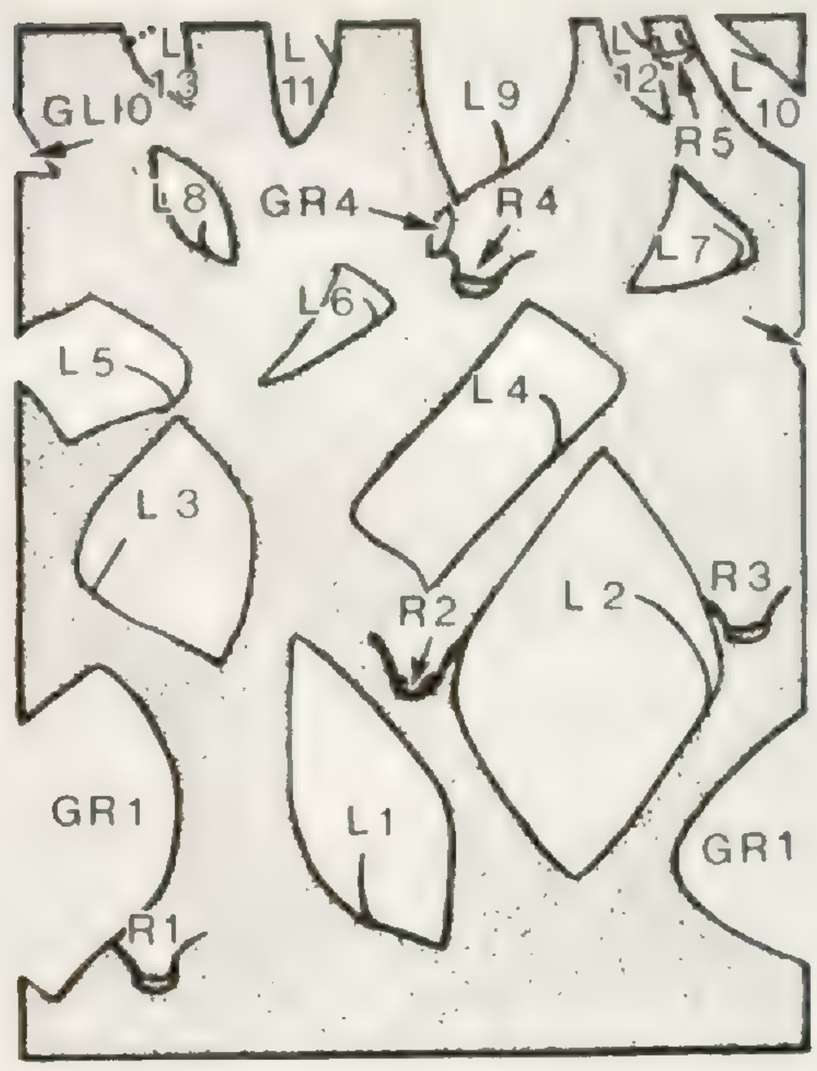

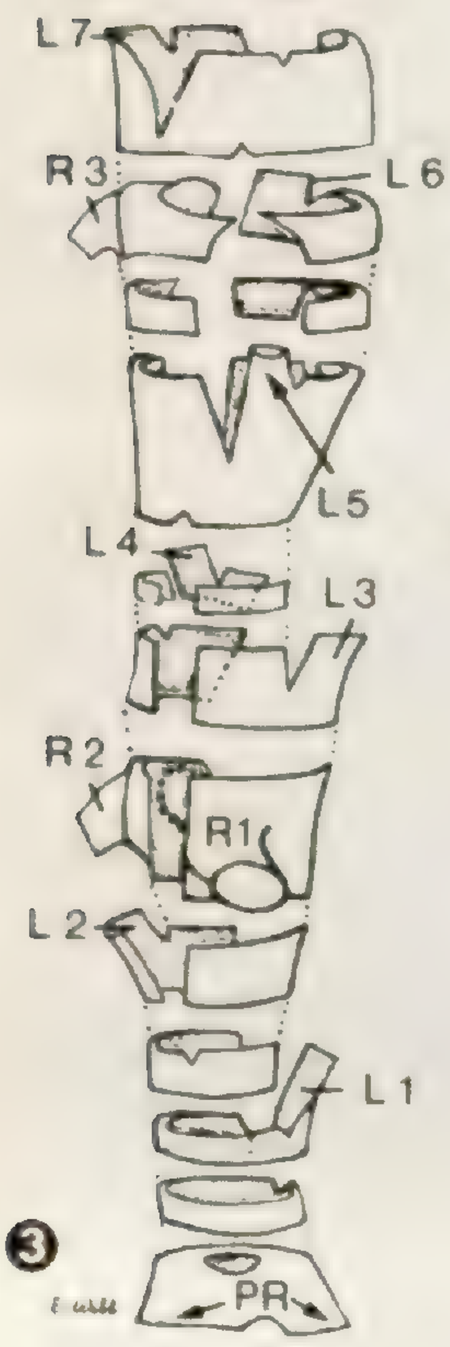

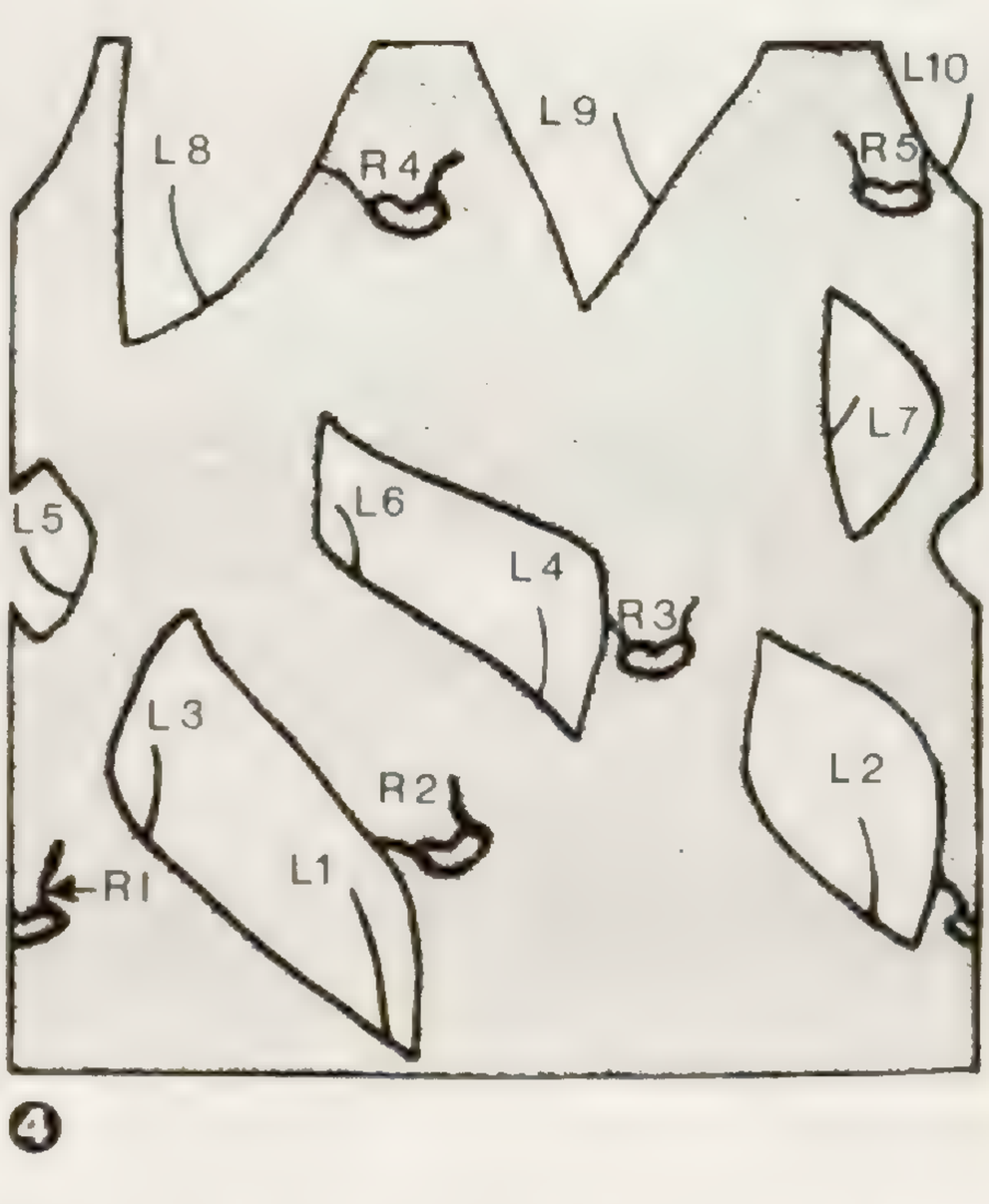

FIGS. 1-4. Stem xylem of *Ophioglossum petiolatum*. FIG. 1. Diagram through procambium of 5th adventitious root is not shown. L = leaf trace; R = adventitious root; PR = xylem of primary root; PRO L13 = procambium of 13th leaf trace. FIG. 2. Xylem of *Fig. 1* opened out to lie in one plane, viewed from the outside, to show spiral pattern formed by gaps. Fifth adventitious root is diagrammed to left of 12th leaf trace where procambium of root is differentiating. GR1, GR4 = gaps associated with 1st and 4th roots; GL5, GL10 = parts of gaps associated with 5th and 10th leaf traces. FIG. 3. Diagram up through 7th leaf trace. Drawn from serially superposed freehand sketches of stem transections. FIG. 4. Xylem cylinder of *Fig. 3* spread in one plane and viewed from the outside.

MATERIALS AND METHODS

The plants used in this study were collected from a greenhouse population at the University of Illinois, Chicago Circle Campus. They have been identified as *Ophioglossum petiolatum* Hooker by Dr. W. H. Wagner, Jr. Clones containing 10 stems were cut apart. Each stem bore 4–13 leaves and was 2.5–6.5 mm in diameter and 3.3–11.5 mm long. The stems were trimmed of petioles and roots, killed and fixed in Craf III (Sass, 1966, p. 18), dehydrated in an ethanol-TBA series (Johansen, 1940, p. 130), embedded in "Tissuemat," serially sectioned at 8 μm, and stained with safranin and fast green. Photographs were made of the basipetal and acropetal ends of each gap and of each place along a gap where a leaf trace diverged. The bundle transections were traced, and tracings were built into three-dimensional drawings of the xylem as in *Figs. 1* and *3*. *Figures 2* and *4* were made by sketching the gap patterns onto paper tubes which then were opened out flat.

DESCRIPTION

Stem anatomy.—At the base of the stem is a protostele of exarch xylem (*Fig. 5*) partially surrounded by phloem and entirely surrounded by endodermis. As it ascends in the stem, the stele gradually expands in diameter and pith appears in its center. An ectophloic siphonostele differentiates which contains mesarch xylem (*Fig. 6*). Phloem forms an incomplete cylinder around the xylem. The Casparian strips of the endodermis are no longer visible. The xylem soon breaks up to form two monarch bundles (*Fig. 7*). At this level there is no longer clear histological evidence of an endodermis.

Stem bundle anatomy.—Each vascular bundle is collateral with endarch xylem in 2–5 layers of tracheids. The phloem in each bundle consists of 1–3 layers of sieve cells. Between the phloem and xylem are parenchyma cells (*Fig. 7*). There is no secondary vascular tissue.

Internodal bundle number.—There are two internodal bundles at the base of the stem (*Fig. 7*). In the internode just below leaf 2, and in the other internodes, the internodal bundle number is 2 or 3. There may be as many as 5 internodal bundles near the apex (*Figs. 1* and *3*).

Pith and cortex.—The pith and the cortex are of parenchyma cells containing starch grains; the grains are fewer in the outer cortex. Intercellular spaces are visible only in the outer cortex.

Symmetry and phyllotaxis.—In the dictyostelic part of the stem, each leaf and root trace has diverged from the edge of a meristele. *Figure 2* shows that traces for leaves 2, 7, and 12 diverge from one side of a gap and traces 3, 8, and 13 diverge from the other side of a gap. Each of these sets of traces enters leaf bases which are in a common orthostichy.[2]

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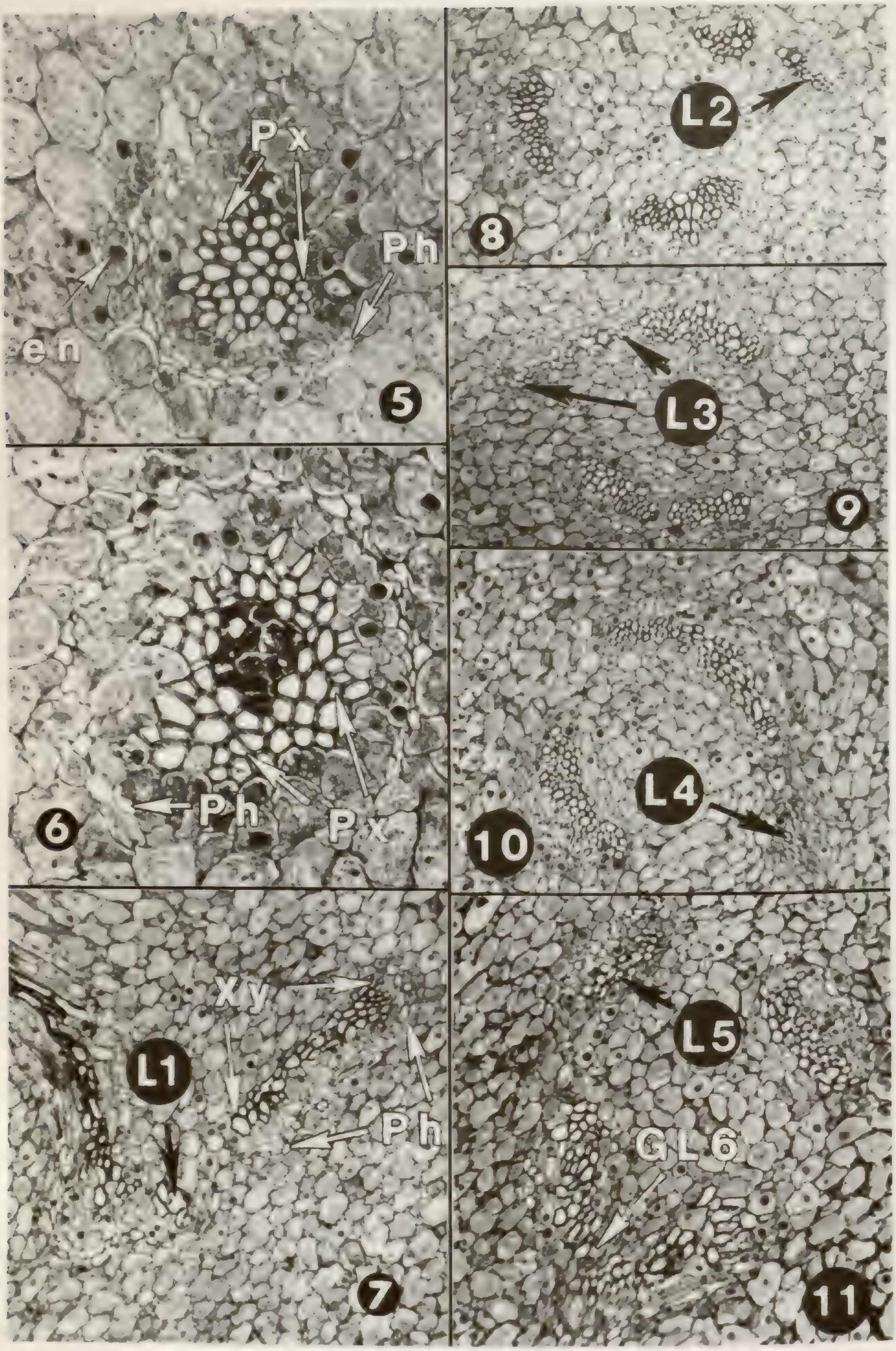
[2] An orthostichy is an approximately vertical succession of leaves up a stem. A parastichy is a succession of leaf bases outward from the apical bud along the path of a logarithmic spiral around the stem. Some parastichies curve downward to the right, and some curve to the left. A parastichy set is the sum of the parastichies on a stem. A phyllotactic fraction is the theoretical angle at which a leaf originates from the stem apex. It is defined as the number of turns of a spiral between two successive leaves on the same orthostichy/the number of orthostichies on the stem (Dormer, 1972, Chapter 4; Steeves & Sussex, 1972, pp. 90–91).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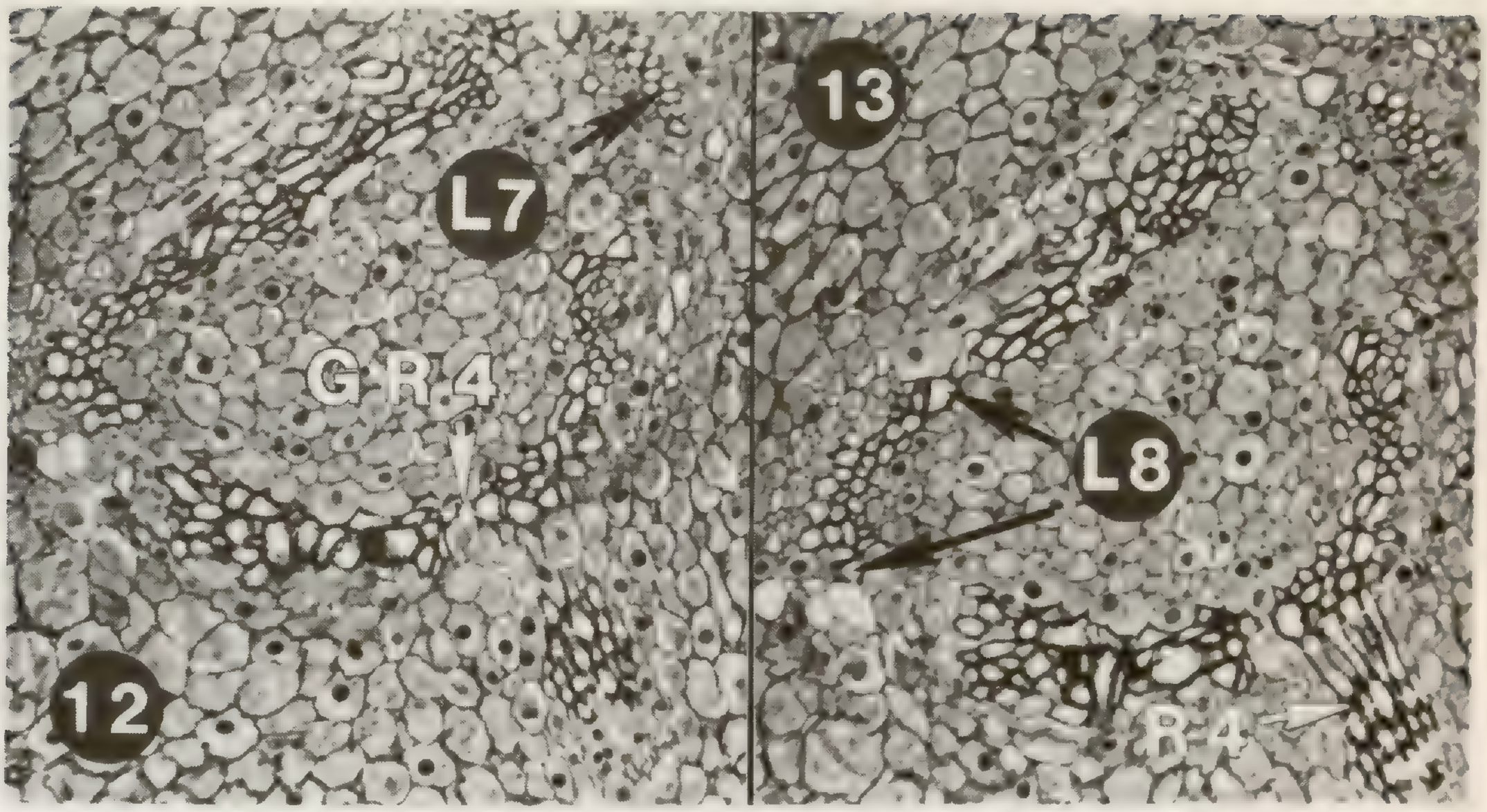

FIGS. 5–13. Stem xylem of *Ophioglossum petiolatum*. Transections of stem in *Figs. 1* and *2* from base of stem upward. en = endodermis, GL6 = gap associated with 6th leaf trace, GR4 = gap associated with 4th root, L1 and L2 = leaf traces, Ph = phloem, Px = protoxylem, R = root trace, Xy = xylem. FIG. 5. Protostele, × 135. FIG. 6. Siphonostele, × 177. FIGS. 7–11. Dictyostele. FIGS. 7–9, × 60. FIG. 10, × 82. FIG. 11, × 77. FIGS. 12–13, × ca. 81.

The phyllotactic fraction is 2/5. Leaf and root gaps occur in a continuous double spiral which inclines to the left in a sinistrorse, or clockwise upward, spiral. The double spiral of gaps reflects the parastichy set of 2+3. Leaf gaps 1, 3, 5, 7, 9, 11, and 13 are in one parastichy spiral. Leaf gaps 2, 4, 6, 8, 10, and 12 are in a second spiral which is parallel to the first. Three spirals intersect these first two at approximate right angles and are formed by leaf gaps, 1, 4, 7, 10, and 13 in the first spiral; gaps 2, 5, 8, and 11 in the second; and gaps 3, 6, 9, and 12 in the third. The gaps are in approximately vertical lines which reflect 5 orthostichies (*Figs. 2* and *4*).

Adventitious roots.—Root traces are associated with gaps (*Fig. 2*, GR1, GR4; *Fig. 4*). Adventitious root traces are attached at the meristele edges. Roots are not consistently associated with leaf bases.

Xylem gaps.—There are gaps in the xylem which have no apparent connection with either leaves or roots. *Figure 1* shows these gaps just below leaf traces 11, 12, and 13, and there is also a short gap in the xylem of the second leaf trace. These incidental gaps occur in some stems but not in others *(Fig. 3)*. Gap length is generally shorter near the apex; however, this is not true of the gap associated with the 9th leaf trace (*Fig. 2*).

Nodal anatomy.—Leaf traces diverge from the edge of a meristele, rather than from the base of a gap. In the stems used in this study, all leaf traces are single. The stem is therefore characterized by a unilacunar 1-trace nodal anatomy in the terminology summarized by Pant and Mehra (1964).

DISCUSSION

It is clear from *Figs. 2* and *4* that the xylem has an orderly gap pattern which reflects leaf origin in parastichies. Root gaps reflect root origin along a counterclockwise spiral up the stem. The place of attachment of each leaf trace, whether at one side or the other of a margin, bears no direct relation to the parastichy spiral in which the leaf trace appears. The margin from which the trace diverges has nothing to do with orthostichy.

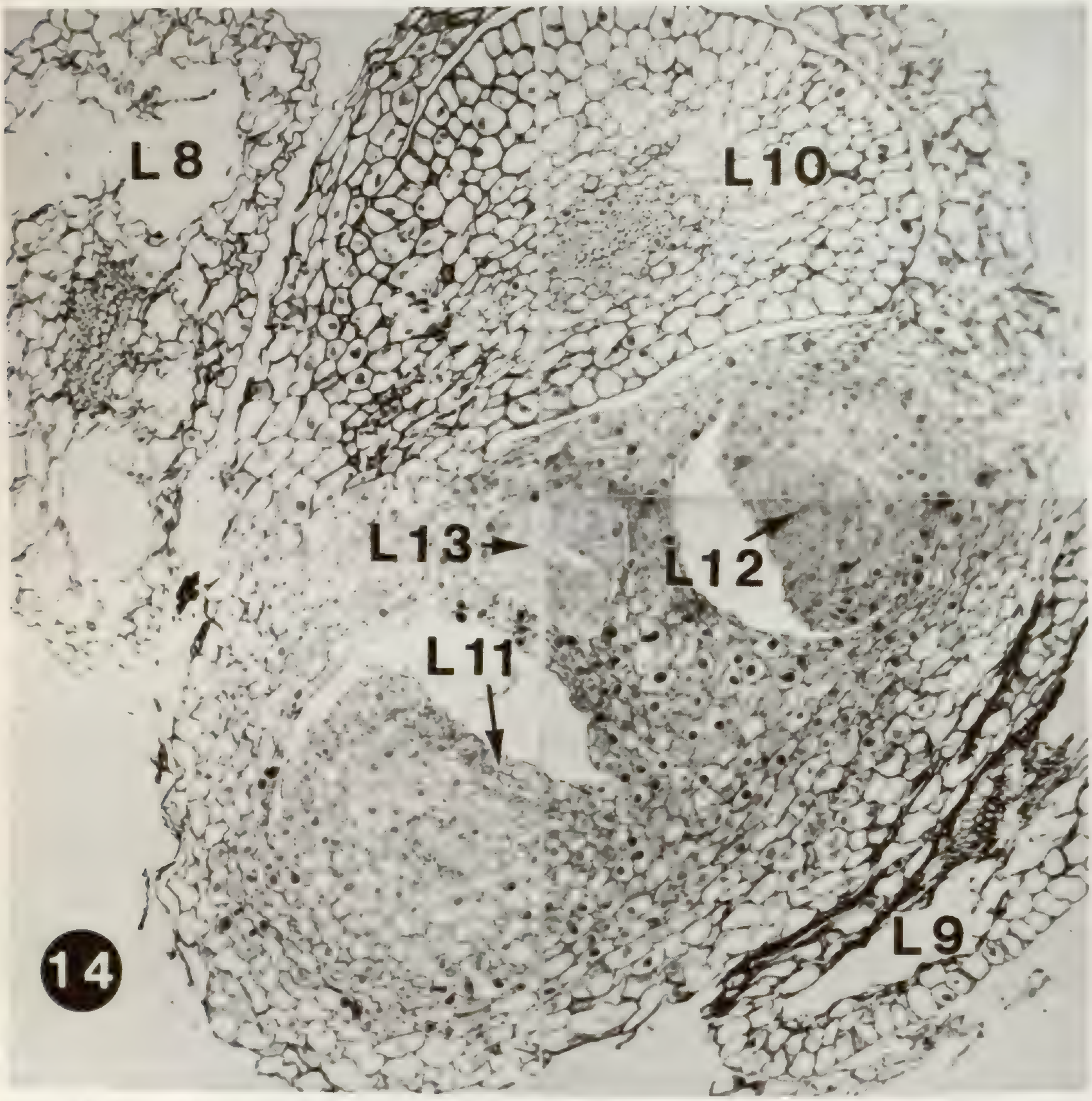

FIG. 14. Stem xylem of *Ophioglossum petiolatum*. Composite photograph of leaf arrangement over apex, × 60.

The findings for *O. petiolatum* are not inconsistent with the descriptions by Church (1901, 1904, 1920) relating to the anatomy of phyllotactic spirals. Speculation as to the significance of the 2+3 pattern formed by the spiraling leaf gaps in the stem xylem of *O. petiolatum* will be limited by the viewpoint of the anatomist.

The intersecting spirals might be viewed as an inevitable consequence of an orderly developmental sequence along a radially symmetrical stem (Dormer, 1972, pp. 87–105, 135, 136). Or the spirals may be artifacts of leaf development, and nothing more. Or they may be cited as purely mathematical phenomena, similar to other arithmetically and geometrically analyzable growth forms throughout the living world, but reflecting nothing concerning phylogeny and relationships to other plants (Thompson, 1944, pp. 919–923, 1022–1025). It is not my intention to become involved in the controversy surrounding these opinions.

At the base of the stem, the adventitious roots do not seem to be associated with leaf traces, but near the apex there appears to be a spatial relation of root to leaf trace which is especially striking in the case of the 9th leaf trace and the 4th root in *Fig. 2*. The adventitious roots seem to fit into the parastichies as accessory to the nearest leaf trace, usually found above the root in question. In the stem of *Fig. 2*, roots 1, 2, and 3 may have arisen near leaf traces 3, 4, and 5 respectively, and then they may have become displaced by stem elongation to places below the leaf traces.

Stevenson (1974) noted the occasional presence of root gaps in *Dennstaedtia cicutaria* but did not offer a possible reason for their presence. There are also root gaps in *O. petiolatum*. The question of how these gaps originate is open. One can speculate, on the basis of Rostowzew (1891) and Poirault (1893), that the root bears a bud within it. Therefore, it is possible that the root gap may be associated with the bud and not with the root.

It may be that near the stem apex, xylem differentiation lags behind the differentiation of leaf traces. Therefore, little or no xylem appears near the apex, and gaps there may be numerous and prominent due to the presence mainly of leaf trace xylem.

Stem anatomy in *O. littorale* and *O. moluccanum* is not known in enough detail to compare these two species with the stem of *O. petiolatum*. Further study of these two species is suggested.

The relatively precise architecture of the stem xylem of *O. petiolatum* is a new finding in anatomy of the Ophioglossaceae. The simple, ordered dictyostele is not similar to the somewhat complex *Ophioglossum* steles shown in dissections of other species. The simplicity and order of *O. petiolatum* dictyosteles reflect an ordered pattern of leaf origin. The simplicity of the stem seems to argue for justification of Bower's (1935, pp. 351–352, 459, 472) conclusion that *Ophioglossum* is a relic.

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SHORTER NOTES

PHOTOPERIODIC CONTROL OF SPORE GERMINATION OF ACROSTICHUM AUREUM.—I have found that the control of spore germination of specimens of *Acrostichum aureum* L. collected from populations in southern Florida is, under the experimental environmental conditions evaluated, a photoperiodic quantitative long-day phenomenon with a critical day length between 8 and 16 hours.

Treatments of spores followed 24 hours of imbibition in 1 ml of Hoagland's nutrient solution with 4 ml of distilled water on two sheets of filter paper in a sterile petri dish. Three replications of each treatment (DD, 4L20D, 8L16D, 12L12D, 16L8D, 20L4D, LL; each × 5, 6, 7, 8, and 9 days) were made. Germination, defined as the emergence of at least one prothallial cell, was detected by examining 100 randomly selected spores in each dish under the 100× of a standard microscope. Treatments were carried out in a white light, adjustable regime incubator at 25±2°C. Six cool-white, 20-watt fluorescent tubes provided a total energy of approximately 4488 ergs/sec·cm^2.

The results of all photoperiod treatments were compared using analysis of variance and the Student–Newman–Keuls' multiple range test. Mean percent germination was found to be statistically the same ($P<0.05$) as a result of white light exposures in the range of 16 hours light and 8 hours dark (16L8D) to 24 hours light (LL), and so these values are depicted in *Fig. 1* as having equal variances.

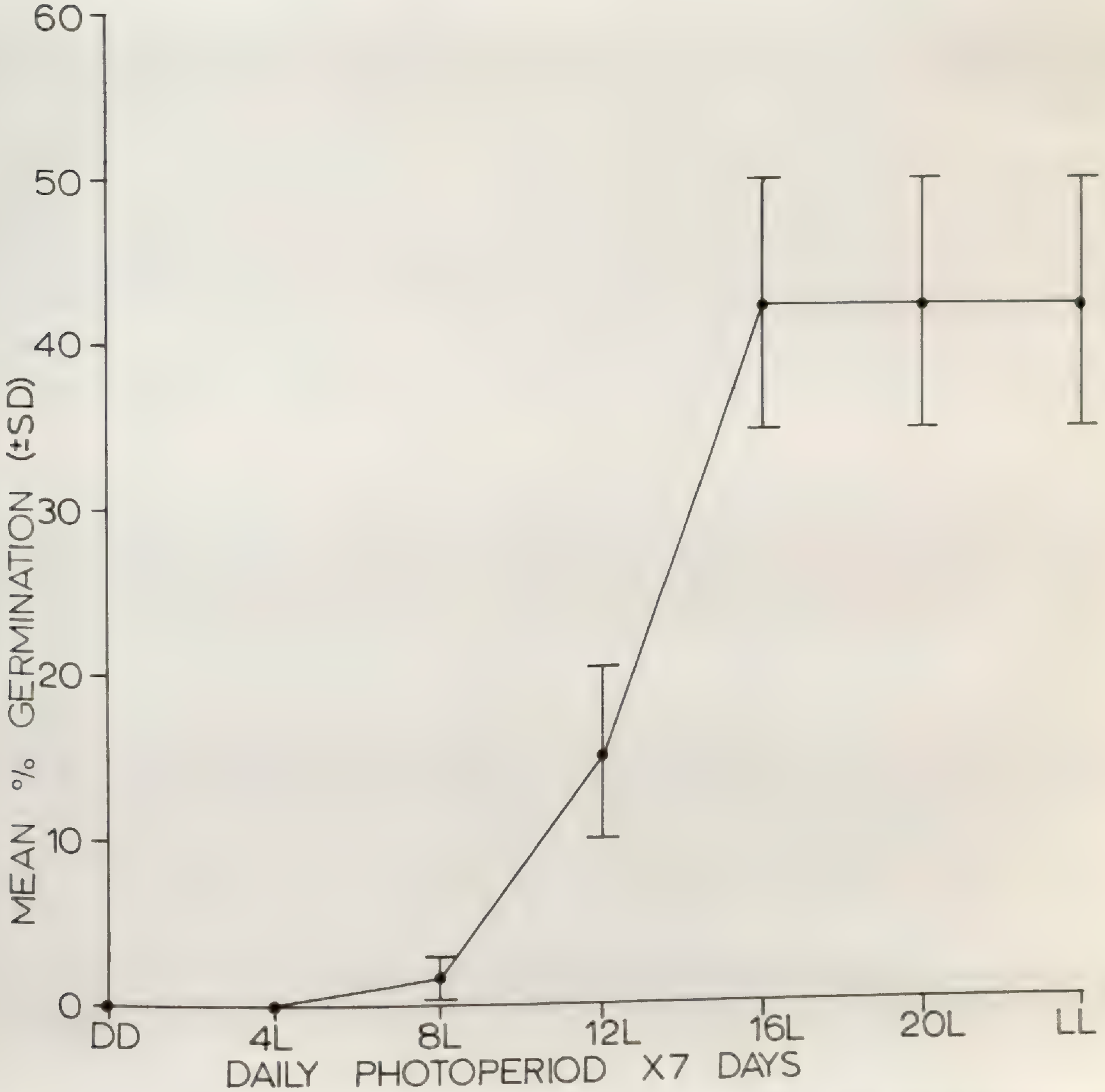

Fig. 1. Mean percent germination (±SD) as a function of photoperiod after the results of photoperiod treatments 16L8D, 20L4D, and LL were found to be statistically equivalent.

The results of the shorter photoperiod treatments differed ($P<0.05$) from the results of the treatments in the 16–24 hours of light group and from each other.

Voucher specimens have been deposited in the herbarium of California State University, Los Angeles (CSLA).—*Thomas W. Eakle, School of Renewable Natural Resources, University of Arizona, Tucson, AZ 85721.*

BLECHNUM OCCIDENTALE NEW TO TEXAS.—The Edwards Plateau of Texas is well known for its unusual ferns. Several tropical ferns, such as *Adiantum tricholepis, Tectaria heracleifolia*,[1] and *Dennstaedtia globulifera*,[2] have been found in this area, which is the extreme northern limit of their ranges. Other unusual ferns and fern-allies are known to occur in central Texas in shallow pools and depressions in the granites and sandstones of the central mineral region. One small mountain in this area, Enchanted Rock (Llano County), has long been a popular site for plant collectors. Among the plants from this mountain are *Pilularia americana, Ophioglossum crotalophoroides*, and *Isoëtes lithophylla*; the last of these apparently is endemic to Llano and Burnet Counties.[1] Turkey Peak, the sister mountain to Enchanted Rock, is the only central Texas location for *Cheilanthes kaulfussii;* and House Mountain, which lies about ten miles northwest, is the only central Texas location for *Notholaena standleyi*. Both species are more commonly found in Trans-Pecos Texas, other parts of the southwestern United States, and in Mexico. Although many areas of the plateau have been studied, it is still possible to find new records in the area.

We wish to report the first collection of *Blechnum occidentale*, the Hammock Fern, from this area. Our collection, *Seigler & Lockwood DS-8932* (ILL) also is the first collection of this largely tropical genus from Texas. The specimen was fully sporiferous when collected on March 23, 1975. This species is typically terrestrial in moist rocky ravines and wooded slopes and only occasionally is an epiphyte; we found it growing in a crevice under large, granitic boulders on Enchanted Rock, Llano County. The horizontal crevice opens to the south and southwest and probably serves to protect the fern from direct sunlight, except in midwinter. Although *B. occidentale* is widely distributed in tropical America, in Mexico it is not known to occur north of Mazatlán in Sinaloa (*Ortega 5092*, US) or Gómez Farías in southern Tamaulipas (*Sharp et al. 52164*, US). It has been reported from two locations in Florida[3] and from one collection in Louisiana.[4] All of the United States populations probably have arisen from spores blown by the wind from Mexico or the West Indies. The Enchanted Rock population probably will persist but not spread because of the lack of proper habitat.—*David S. Seigler and Tommie E. Lockwood, Department of Botany, University of Illinois, Urbana, IL 61801.*

---

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Trichomanes petersii in Louisiana

CHARLES M. ALLEN*,[1]

The inclusion of the filmy fern *Trichomanes petersii* Gray in the Louisiana flora was previously based on a 1924 collection from near Covington in St. Tammany Parish (Brown & Correll, 1942). I am reporting seven new locations for this fern in Louisiana. Throughout most of its range, *T. petersii* grows on rocks or soil and is rarely reported as an epiphyte. But in all Louisiana locations, it was epiphytic.

I found *T. petersii* on Southern Magnolia (*Magnolia grandiflora* L.) and on American Beech (*Fagus grandifolia* Ehrh.). On American Beech the fern usually occurs as a small population (ca. 25 cm^2 or less) very close to the ground, usually on the buttress sides. On Southern Magnolia it usually forms large populations (ca. 900 cm^2 or more) and is 3–10 dm above the base of the tree. In one location, the fern was about 3.5 m above the tree base. Southern Magnolia seems to be the preferred habitat; I have found 10 populations on it but only five on American Beech.

The trees are apparently old, usually very large, and are usually located very close to a stream, often on the natural levee. In all locations there was a dense understory of evergreen shrubs such as *Illicium floridanum* Ellis and *Symplocos tinctoria* (L.) L'Her. At one collection site *Ilex coriacea* (Pursh) Chapman was found.

On the tree trunk with the fern there are many bryophytes, usually the Resurrection Fern *Polypodium polypodioides* (L.) Watt., and the Green-fly Orchid *Epidendrum conopseum* R. Br. Some of the commonly associated mosses include: *Anomodon attenuatus* (Hedw.) Hub., *Herpetineuron toccoae* (Sull.) Card., and *Schlotheimia rugifolia* (Hook.) Schwaegr. Liverworts such as *Mastigolejeunea auriculata* (Wils. & Hook.) Schiffn., *Metzgeria myriopoda* Lindb., and *Plagiochila dubia* Lindenb. & Gott. were usually associated with the fern.

One of the most interesting aspects was the number of bryophytes that were epiphyllously on the filmy fern fronds. Small (1938) reports similar epiphyllous bryophytes from *Trichomanes petersii* collections in Florida. The liverwort *Metzgeria myriopoda* was the most common species of bryophyte observed growing on the fern fronds; others were *Cololejeunea cardiocarpa* (Mont.) Steph., *Lejeunea cladogyna* Evans, *Plagiochila dubia*, and *Radula obconica* Sull. Mosses observed growing on the fern fronds included *Anomodon attenuatus*, *Clasmatodon parvulus* (Hampe) Sull., and *Herpetineuron toccoae*.

Trichomanes petersii apparently is widespread in eastern Louisiana but is nowhere abundant. It is able to grow in the moist and protected habitat afforded by smooth-barked trees growing in close proximity to streams with a dense understory of evergreen shrubs. At most sites, there was spore production at the time of collection.

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* Department of Biology, University of Southwestern Louisiana, Lafayette, LA 70501.

[1] I am indebted to Garrie Landry, Alan Neuman, and Alan Broussard for their assistance in the research.

Volume 65, number 3, of the JOURNAL was issued October 8, 1975.

Unless otherwise noted, the collection numbers cited below are mine and the specimens are in the Herbarium of the University of Southwestern Louisiana (LAF).

EAST BATON ROUGE PARISH: On *Magnolia grandiflora* along small creek off O'Neal Lane ca. 0.5 mile N of junction with Interstate Highway 12, 13 Feb 1975, *Landry 75001* (LAF, LSU).

EAST FELICIANA PARISH: On *Fagus grandifolia* along Spring Branch just west of the Amite River off Hwy. 10 ca.10 miles E of Clinton, 21 Feb 1975, *6314*.

LIVINGSTON PARISH: On *Magnolia grandiflora* along West Hog Branch ca. 1.5 miles W of Magnolia and 5.5 miles NW of Holden, Sec 32 T5S R5E, 31 Jan 1975, *6282*.

ST. HELENA PARISH: On *Fagus grandifolia* along East Hog Branch ca. 2.5 miles WSW of Montpelier, Sec 49 T4S R5E. 31 Jan 1975, *6289*.

ST. TAMMANY PARISH: On *Magnolia grandiflora* along Tchefuncte River ca. 4.5 miles W of Folsom on Hwy. 40, Sec 39 T5S R10E, 11 Feb 1975, *6309*.

TANGIPAHOA PARISH: On *Magnolia grandiflora* near Tangipahoa River off Hwy. 16 ca. 1.5 miles east of Amite, Sec 51 T4S R7E, 10 Feb 1975, *6301*.

WASHINGTON PARISH: On *Magnolia grandiflora* along edge of seepage area ca. 2.5 miles W of Enon, Sec 56 T4S R11E, 11 Feb 1975, *6306*.

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SMALL, J. K. 1938. Ferns of the Southeastern States. Science Press, Lancaster, Pa.

THE FERN GUIDE, by Dr. Edgar T. Wherry, is now available in paperback reprint. $3.00 each including postage; quantity discounts available. Morris Arboretum, 9414 Meadowbrook Ave., Philadelphia, PA 19118.

A Staghorn Fern (Platycerium) Hybrid[1]

BARBARA JOE HOSHIZAKI*

A hybrid of *Platycerium* has been developed by Mr. Tom Mentelos of Fantastic Gardens, Miami, Florida. The parents of this hybrid are *P. stemaria* (Pal. Beauv.) Desv. and *P. superbum* Jonch. & Hennipm. (formerly known as *P. grande* (Cunn.) J. Smith). Mr. Mentelos obtained the hybrid by planting prothalli of the parents in alternate rows. I examined only one hybrid plant of the three reportedly obtained from the sowing. Spores produced by this hybrid are greatly distorted, although a few of normal shape may be found; these probably account for the reports of viability of this hybrid. Plants grown from these spores are said to vary in appearance, but when small they are silvery and like *P. superbum*. This hybrid can be known as:

Platycerium × mentelosii Hoshizaki, hybr. nov.

Planta hybrida inter *P. stemariam* et *P. superbum* interjecta. A *P. superbo* areis sporangiferis duobus et fasciculis vascularibus dissitis in stipitibus frondium fertilium differt. A *P. stemaria* marginibus superioribus lobatis frondium basilium et sclerenchymate annulariformi fusco in stipitibus frondium fertilium differt.

TYPE: From material cultivated at Fantastic Gardens, Miami, Florida, *Hoshizaki 73-31* (LA).

The hybrid plant (*Fig. 1*) is in overall aspect intermediate between its parents. The rhizome scales are lanceolate, acuminate, tannish, often with a darker center, and with margins having a sparse and irregular distribution of papillae and hairs. The hairs are one to several cells long and occasionally are gland-tipped. The marginal cells of the scales occasionally are oriented in a different direction from the central cells (flabelloid). The base fronds are oblong, ca. 80 cm long, 45 cm wide at the base, and 70 cm wide at the apex, and are apically foliaceous and free of the substrate. Their upper margin is irregularly forked, but the margin around the bud is ruffled. The fertile fronds are several times forked, ca. 60 cm long and 75 cm wide. Their stipes in cross-section have a dark, sclerotic ring of tissue, with the vascular bundles scattered within the ring (*Fig. 2*). The area of the lamina below the primary fork is wide and wedge-shaped; the lamina divisions are very irregular and mostly become successively shorter and narrower towards the blade apex (*Fig. 3*). There are two broad sporangial patches, each ca. 20 cm long and 20 cm wide. The patches are roughly crescent-shaped, irregularly margined, and submarginal, and are situated around the secondary sinuses and extend up into the next fork (*Fig. 3*). The spores are abortive.

Platycerium × mentelosii can be distinguished from *P. stemaria* by its lobed rather than entire base fronds and from *P. superbum* by having two rather than usually one sporangial patch. Also, the scattered vascular bundles and ring of sclerotic tissue are features not found together in either parent. *Platycerium*

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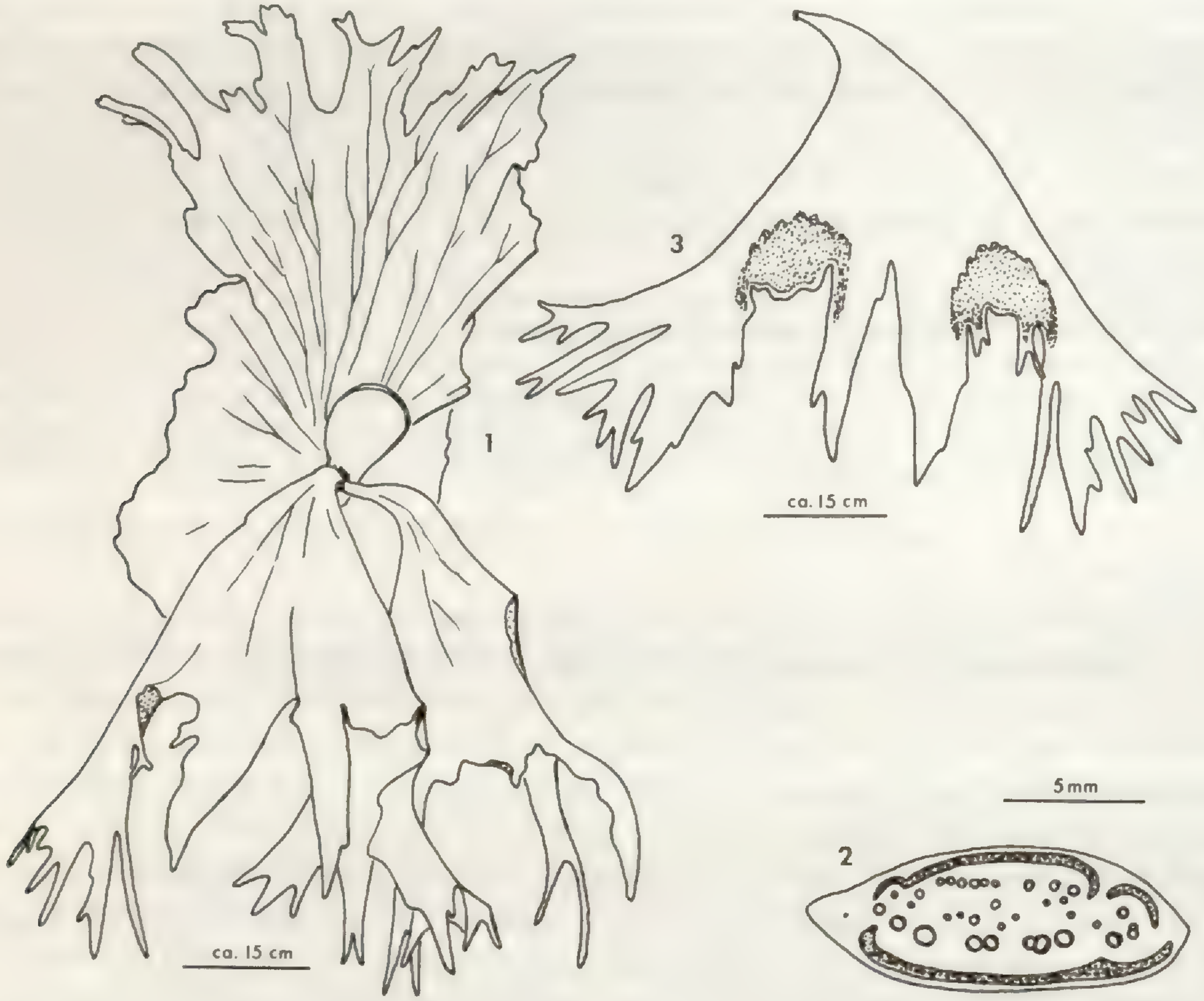
[1]Thanks are due Mr. Emilo de Mesa for supplying the photographs from which the habit and frond drawing were made.

stemaria has its many vascular bundles scattered and lacks a sclerotic ring. *Platycerium superbum* has its fewer vascular bundles arranged in a circle and has a dark, sclerotic ring of tissue. Both *P.* × *mentelosii* and the true *P. grande* are similar in having two sporangial patches. However, *P. grande* has the same type of vascular bundle arrangement in the stipe as does *P. superbum* and also has regularly shaped lobes on the base fronds and on the fertile fronds.



Platycerium × *mentelosii* cv. *Fantastic Gardens*. FIG. 1. Habit. FIG. 2. Stipe of fertile frond, cross-section. FIG. 3. Fertile frond.

The "International Code of Nomenclature of Cultivated Plants" (Art. 19) requires that any interspecific hybrid introduced into cultivation must have a cultivar name in addition to its hybrid name, even if only one cultivated hybrid plant is known. Therefore, it is necessary to provide a cultivar name as follows:

Platycerium × mentelosii cv. Fantastic Gardens, Hoshizaki, cv. nov.

The base frond foliaceous, the surface undulate, the upper margin irregularly forked into short lobes. The fertile frond to ca. 5 times forked, the area below the primary fork broad, wedge-shaped, the central divisions of the frond less divided than the divisions on the sides of the frond, all the divisions irregular in shape, the ultimate divisions mostly merely irregular lobes.

That hybrids typically are intermediate in overall appearance between their parents is well known. However, a thorough examination of the structure of the

hybrid may demonstrate great variability. In *P.* × *mentelosii* a number of features were the same as in one parent or the other. Roughly a third of all features examined were like *P. stemaria*, a third like *P. superbum*, and a third intermediate. Very few features were entirely different from the parents (*Table 1*).

TABLE 1. FEATURES OF *Platycerium* × *mentelosii* AND ITS PARENTS.

Feature	*P. stemaria*	*P.* × *mentelosii*	*P. superbum*
Rhizome scale width	1 mm	3 mm	6 mm
Rhizome scale apex	filiform	filiform	rounded
Rhizome scale hairs	marginal	marginal	marginal to submarginal
Rhizome scale marginal cells	not flabelloid	partially flabelloid	flabelloid
Rhizome scale texture	not papery	not papery	papery
Base frond upper margin	entire	lobed	lobed
Stipe meristele arrangement	polycyclic	polycyclic	dictyostelic
Stipe meristele number in largest stipe	60	34	22
Stipe, fiber-like cells	not sclerotic	sclerotic	sclerotic
Stipe cortex, parenchyma layers	8	5	14
Stomates on lower epidermis of base fronds	present	absent	absent
Stomate density on fertile frond (per mm^2)	84	38	39
Fertile frond palisade cells	present	absent	absent
Upper epidermal cells of fertile frond, l/w[1]	1.3	1.3	1.0
Trichome stalk number of cells[1]	4 or 5	1	1
Trichomes modified, dark and turgid	absent	absent	present
Paraphysis diameter[1]	0.5mm	0.4mm	0.2mm
Sporangium development	weakly mixed	gradate	gradate
Sporangium area specialization	unspecialized	partly specialized	specialized
Sporangium area location	subapical	subapical-medial	medial-basal
Sporangium area, number	2	2	1
Sporangium stalk, uppermost cell length[1]	0.05mm	0.09 mm	0.12mm
Sporangium stalk, longest	0.2mm	0.4mm	1.4mm
Sporangium case length[1]	0.30mm	0.32mm	0.41mm
Annulus cells, total number[1]	26	33	34
Annulus cells, indurate number[1]	18	22	21
Annulus cells, nonindurate number[1]	8	11	13
Annulus cells, nonindurate number opposite lip side[1]	0	2	1
Receptacle distance	0.6mm	0.5mm	0.4mm
Spore development	normal	aborted	normal

[1] Average of 10 samples.

Features were selected for examination because they were found to be useful in separating the species of the genus, particularly the parents.[2] How these features are distributed in the offspring of the hybrid will be interesting and may be helpful in explaining some of the variation seen in other *Platycerium* species.

[2] Hoshizaki, B. J. 1972. Morphology and phylogeny of Platycerium species. Biotropica **4**: 93–117.

The Ferns and Fern-allies of Cocos Island, Costa Rica

LUIS DIEGO GÓMEZ P.*

Cocos Island, in the Pacific Ocean at 5°32′57″ N Lat. and 86°59′17″ W Long., is the only extra-continental possession of Costa Rica. It is uninhabited and lies some 500 km south-southwest of Costa Rica and about 830 km north-northeast of the Galápagos Islands.

The island is known from early times. In 1541, N. Desliens included it in one of his maps under the name of "Yle des Cocques," a name probably based on the abundance of coconut palms found there. It was for a long time a favorite anchorage of pirates and buccaneers, as it was far from Spanish garrisons on the continental shores. In more recent times it has been a stop for whalers in search of fresh water and game. Cocos Island is better known for the many stories telling of hidden treasure than for its fauna and flora. The paucity of floristic studies is well summarized by Hertlein (1963).

The island is of volcanic origin, as evidenced by the abrupt topography and the nature of its rocks. The soils are poor, mostly clayish, and not very deep. Nevertheless, they support a luxuriant vegetation which thrives in the almost constant rainfall that averages about 7000 mm per year.

The ferns and fern-allies have been reported in rather fragmentary fashion by a few botanists who stopped at one of the two large bays (Chatham and Wafer) for a few hours on their way to or from the Galápagos Islands or during more general oceanographic researches of the western coasts of tropical America. Some records are those of Hemsley (1882–1886), Robinson (1902), Stewart (1912), Svenson (1935), and Fosberg and Klawe (1966). I have been on the island for two expeditions which totalled fifteen weeks.

As of now, the Pteridophyta of Cocos Island is known to include 60 species, of which six are endemic:

Cyathea alfonsiana L. D. Gómez, *C. notabilis* Domin, *Lycopodium brachiatum* Maxon, *Thelypteris (Goniopteris)* n. sp., *Trichipteris nesiotica* (Maxon) Tryon, and *Trichomanes capillaceum* var. *cocos* (Christ) L. D. Gómez.

One of them, *Asplenium macraei* Hook. & Grev., is known from Samoa and Hawaii. This is a variable species with several varieties recognized. The Cocos material is variable itself, and cannot be referred to a particular variety until studied further.

Forty-three are known from Costa Rica, Panama, and northern Pacific coastal Colombia; many of these, of course, range beyond these areas in tropical America:

Acrostichum aureum L., *Adiantum latifolium* Lam., *Anetium citrifolium* (L.) Splitg., *Asplenium abscissum* Willd., *Campyloneurum phyllitidis* (L.) Presl, *Ctenitis sloanei* (Poeppig) Morton, *Danaea nodosa* (L.) J. E. Smith, *Dennstaedtia obtusifolia* (Willd.) Moore, *Dicranopteris pectinata* (Willd.) Underw., *Grammitis blepharodes* (Maxon) Copel., *G. cultrata* (Willd.) Proctor, *G. serrulata* (Swartz) Swartz, *Hymenophyllum hirsutum* (L.) Swartz, *H. polyanthos* (Swartz) Swartz, *Hypolepis repens* (L.) Presl, *Lindsaea lancea* (L.) Bedd. var. *lancea*, *Lycopodium cernuum* L., *L. linifolium* L., *Meniscium*

*Herbario Nacional, Museo Nacional de Costa Rica, Apartado 749, San José, Costa Rica.

serratum Cav., *Nephrolepis biserrata* (Swartz) Schott, *Oleandra nodosa* (Willd.) Presl, *Phlebodium aureum* (L.) J. Smith, *Pityrogramma calomelanos* (L.) Link, *Pleopeltis astrolepis* (Liebm.) Fourn., *Polybotrya aucuparia* Christ, *P. osmundacea* Humb. & Bonpl. ex Willd., *Polypodium chnoodes* Spreng., *Psilotum nudum* (L.) Pal. Beauv., *Pteris biaurita* L., *Saccoloma elegans* Kaulf., *Selaginella horizontalis* (Presl) Spring, *Tectaria antioquiana* (Baker) C. Chr., *T. incisa* Cav., *Thelypteris balbisii* (Spreng.) Ching, *T. quadrangularis* (Fée) Schelpe var. *quadrangularis*, *Trichomanes collariatum* v. d. Bosch, *T. crispum* L., *T. curtii* Rosenst., *T. diaphanum* H.B.K., *T. elegans* L. C. Rich., *T. kapplerianum* Sturm in Mart., *T. membranaceum* L., and *Vittaria graminifolia* Kaulf.

Four are known from Costa Rica and Colombia, but are not yet known from Panama; some of these also range beyond Costa Rica and Colombia:

Elaphoglossum latifolium (Swartz) J. Smith, *E. plumosum* (Fée) Moore, *Polybotrya cervina* (L.) Kaulf., and *Trichomanes ankersii* Parker in Hook. & Grev.

Six are known from Costa Rica and Panama, but are not yet known from Colombia; some of these also range beyond Costa Rica and Panama:

Elaphoglossum apodum (Kaulf.) Schott, *E. crinitum* (L.) Christ, *Tectaria mexicana* (Fée) Morton, *Thelypteris decussata* (L.) Proctor, *Trichomanes angustifrons* (Fée) W. Boer in Kramer, and *T. galeottii* Fourn.

The vascular cryptogams clearly have neotropical affinities, but with reduced endemism (6 species, 10% of the pteridophyte flora). The flowering plant flora, which has 30% or more endemism, shows a decided affinity with tropical South America.

Of the 60 species of pteridophytes, 37 (61.6%) are typical of tropical and subtropical wet forests, whereas the remaining 23 species are of varied habitats and distributions. Epiphytes number 24 (40%), 31 (51.7%) are terrestrial, and the remaining 5 (8.3%) are ambiguous as to their habitat.

In regard to their distribution within the island, the vegetation on Cocos can be divided into a littoral type (0–50 m altitude) and a montane type (100–900 m altitude), with an intermediate area (50–100 m altitude) lying between them.

The littoral type is well developed in the narrow valleys of the main bays and larger coves, where the dominant species are *Erythrina fusca*, *Cocos nucifera*, *Anonna glabra*, Rubiaceae, and Solanaceae, with the highest diversity of low, herbaceous vegetation (Bromeliaceae, Gramineae, Leguminosae, Malvaceae, and Orchidaceae). It includes two subtypes, the swamp with *Anonna*, *Cassipourea* (replacing the continental *Rhizophora*), and *Acrostichum aureum*, and solid, non-swampy areas not subject to periodic or tidal flooding, where *Ctenitis*, *Dicranopteris*, *Polybotrya*, *Psilotum*, *Selaginella*, *Thelypteris*, and most of the epiphytes grow.

The montane type has *Saccoglottis*, Palmae, and Lauraceae predominant. The vegetation of the forest floor is thin, and there is a rich and diverse bryophytic flora including the mosses *Callicostella*, *Calymperes*, *Fissidens*, *Meteoriopsis*, *Pilotrichum*, and *Thuidium*, and the hepatics *Anthoceros*, *Ceratolejeunea*, *Frullania*, *Macrolejeunea*, *Plagiochila*, and *Radula*. The conspicuous ferns are Cyatheaceae, *Danaea*, and *Dennstaedtia* along water courses. Hymenophyllaceae and *Thelypteris decussata* occur in the shady forests, and *Elaphoglossum crinitum* and *Lycopodium linifolium* are the principal epiphytes.

The intermediate area is an area of mixed vegetation. It is rich in Melastomaceae and Lauraceae, the prominent tree is the endemic *Cecropia pittieri* (Moraceae), and the ground vegetation is almost exclusively *Calyptrocarya* (Cyperaceae) and *Selaginella horizontalis*. Hymenophyllaceae and *Anetium citrifolium* also are found in the intermediate area.

A detailed account of the taxonomy, ecology, and distribution of Cocos Island ferns and fern-allies is forthcoming (Gómez P., 1976).

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Reproductive Biology and Gametophyte Morphology of Acrostichum danaeifolium from Mexico

ROBERT M. LLOYD and T. LEE GREGG*,[1]

Most homosporous ferns produce hermaphroditic, haploid gametophytes which arise from a single haploid spore by a series of mitotic divisions. As a result, the male and female gametes from a single gametophyte are genetically identical, barring mutations. Therefore, sporophytes produced by self-fertilization (fusion of sperm and egg from a single gametophyte) can be considered to be genetically homozygous. Although most species produce gametophytes which have the capability for hermaphroditism, several factors of their reproductive biology influence the probability of self-fertilization occurring. These factors include time of maturation of archegonia relative to antheridia, orientation of archegonial necks, density and spatial arrangement of gametophytes (especially when coupled with an antheridogen or other chemical substance which increases the number of unisexual male gametophytes in the population), and presence of deleterious recessive genes which are lethal or sublethal in the homozygous condition (genetic load as used here) and which can prevent production of viable sporophytes following selfing (Klekowski & Lloyd, 1968; Klekowski, 1969a, 1971; Lloyd, 1974a, b, c).

Due to the ability of fern gametophytes to form completely homozygous zygotes, it is possible to screen sporophytes for deleterious recessive genes which are active following syngamy and in the first stages of sporophyte ontogeny (*Figs. 19–23*). These genes are usually expressed as abortive zygotes, abortive embryos which appear as swollen tissue within the archegonium, small and abnormal sporophytic tissue, or abnormalities in the production of the first few fronds or roots (Ganders, 1972). Data of this type, when correlated with gametangia ontogeny, antheridogen studies, and population dynamics of the gametophyte generation have allowed us to sample populations of plants and to determine their probable mating systems and relative degrees of genetic heterozygosity. To date, only a few species have been sampled intensively, including *Osmunda regalis* (Klekowski, 1970a, 1973) and *Ceratopteris thalictroides* (Klekowski, 1970b). In some cases it has been possible to predict patterns of population variability and to correlate specific mating systems with specific ecological parameters (Lloyd, 1974b).

Two levels of mating are recognized in homosporous ferns, intragametophytic and intergametophytic. Intragametophytic selfing is by definition self-fertilization within single gametophytes with the resulting intralocus genetic homozygosity. Intergametophytic mating results in various levels of heterozygosity depending on the origin of the gametes. Fusion of gametes originating from separate gametophytes but these in turn from spores of a single sporophyte (inter-

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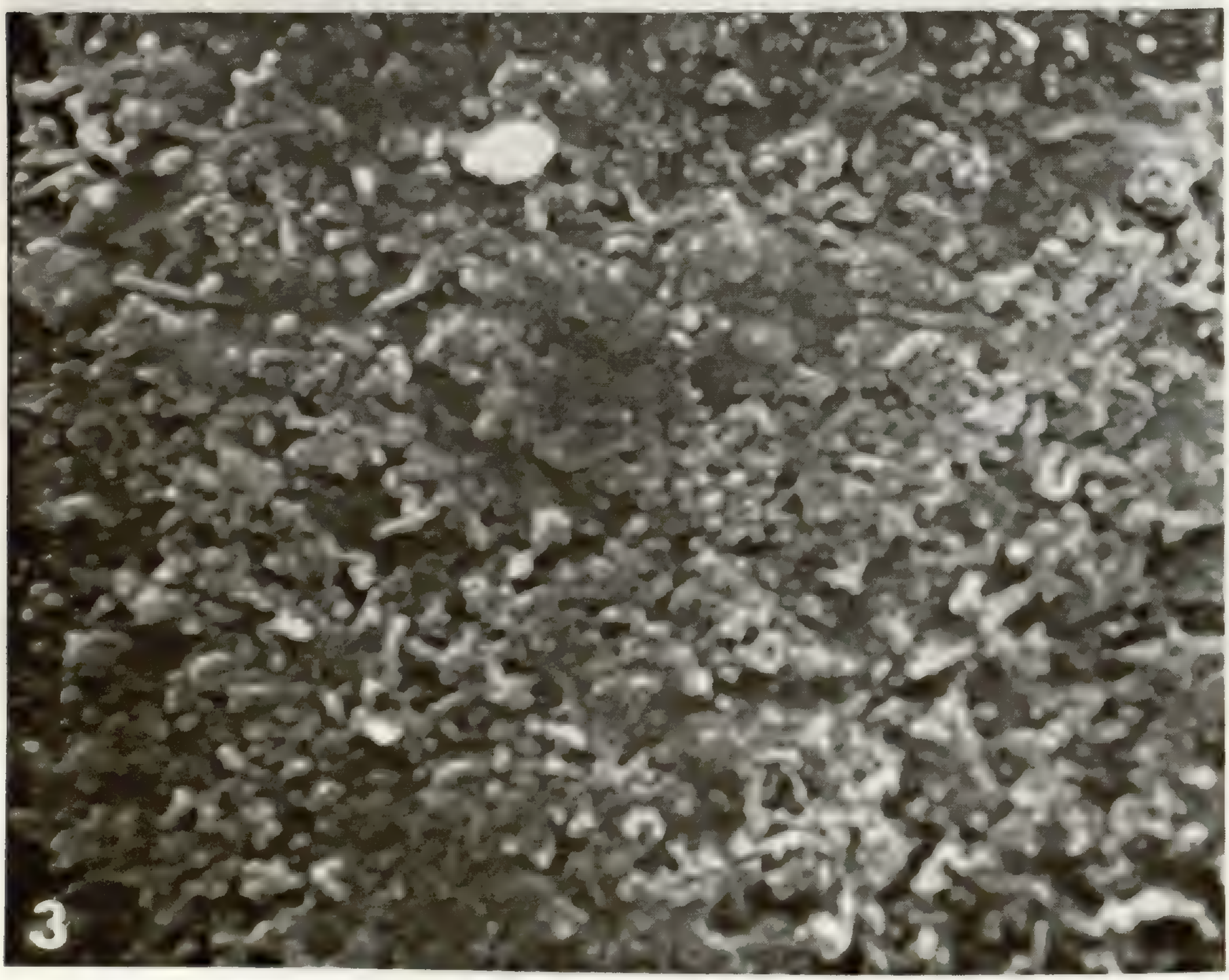


FIGS. 1–3. Spores of *A. danaeifolium*. FIG. 1. Colombia, *H. H. Smith 2216* (UC), × 1000. FIG. 2. Panama, *Killip 2820* (UC), × 1000. FIG. 3. Surface view showing papillae, Colima, Mexico, *Alava & Cook 1703* (UC), × 8000.

gametophytic selfing) is analogous to inbreeding in flowering plants and yields sporophytes with decreased levels of genetic heterozygosity; fusion of gametes originating from gametophytes originating from spores from two different sporophytes (intergametophytic crossing) yields sporophytes with increased or maintained levels of genetic heterozygosity (analogous to outbreeding in flowering plants).

The genus *Acrostichum* consists of at least two species, including *A. aureum* L., distributed circumtropically, and *A. danaeifolium* Langsd. & Fisch., distributed in the tropics and subtropics of the New World. The species are distinguished by the distribution of fertile pinnae on the fertile fronds. Fronds of *A. aureum* are fertile only near the tip, whereas those of *A. danaeifolium* are fertile more or less throughout. In addition, there are minute differences in other sporophyte characteristics, in spore surface features, and in habitat requirements.

MATERIALS AND METHODS

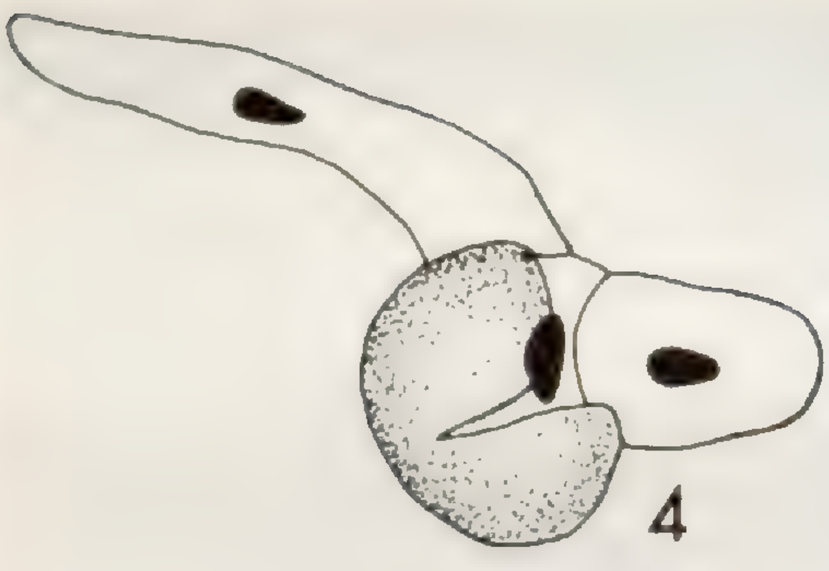
Spores of *A. danaeifolium* were collected from plants comprising four populations at Km. 215, 203, 201, and 162, west of Villahermosa in Tabasco, Mexico, during July, 1973. Spores were sown and gametophytes grown on inorganic nutrient medium solidified with 1% agar (for composition see Klekowski, 1969b) in 100 × 15 mm petri dishes (stock plates) or on sterile soil medium. Gametophytes were grown under continuous illumination by fluorescent and incandescent lamps at an intensity of 210–290 ft-c, at about 20°C. Prothallial morphology was studied using living material, as well as that mounted in Hoyer's medium mixed with acetocarmine. Methods utilized in individual experiments are described below.

Spores utilized in the scanning electron micrographs were dry mounted on double-stick mending tape, coated with gold, and observed with an Hitachi HHS-2R Scanning Electron Microscope in the Department of Botany at Ohio University.

RESULTS

Spores of *Acrostichum danaeifolium* are tetrahedral and vary from 44 to 72 (mean = 54.0) μm in diameter. The spore surface is minutely roughened and bears small, projecting papillae (*Figs. 1–3*). In all plants examined the spore number per sporangium was about 64.

Spore germination usually is initiated by the emergence of the rhizoid through the germinal furrows of the triradiate ridge five to six days following sowing (*Fig. 4*). Lateral cell divisions of the one-dimensional filament ultimately produce a filament 5–9 cells long before initiation of two-dimensional growth (*Figs. 5, 6*). Two-dimensional growth is initiated eight to nine days after sowing by a longitudinal division in a more basal cell about 4–8 cells behind the terminal cell (*Figs. 7–9*). Subsequent longitudinal divisions throughout the filament result in a two-dimensional filament composed of two-ranked cells, except for the terminal and basal cells (*Fig. 10*). In some cases, cells with initial longitudinal divisions near the base of the filament will again divide, producing a three-dimensional structure (*Fig. 8*). Further longitudinal divisions in the cells of the two-dimensional filament, appearing to initiate in cells in the basal region, produce a broadly linear or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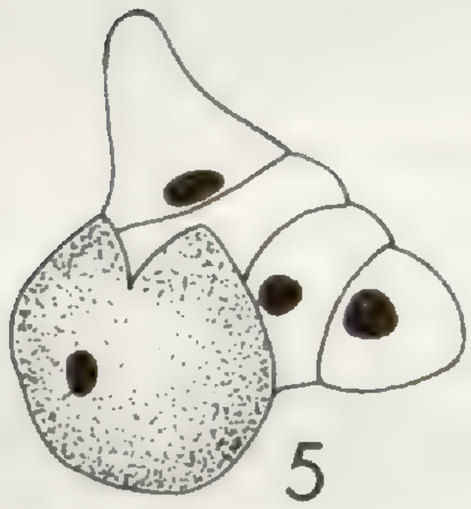
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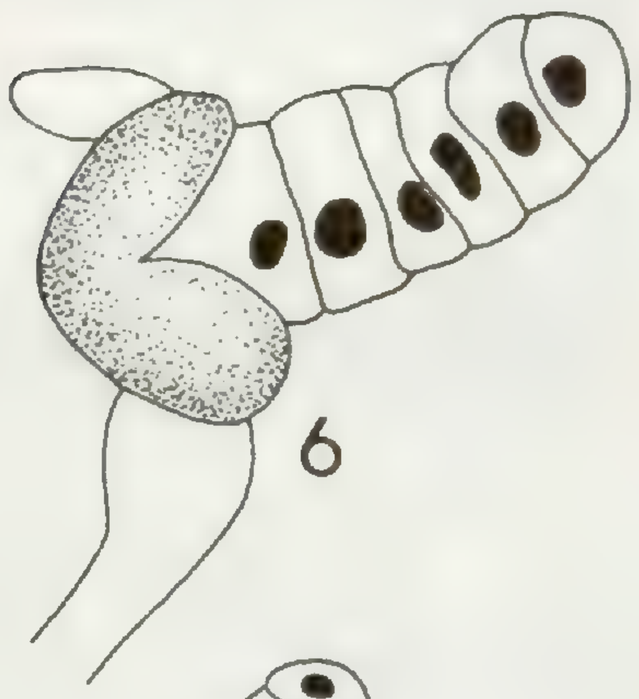
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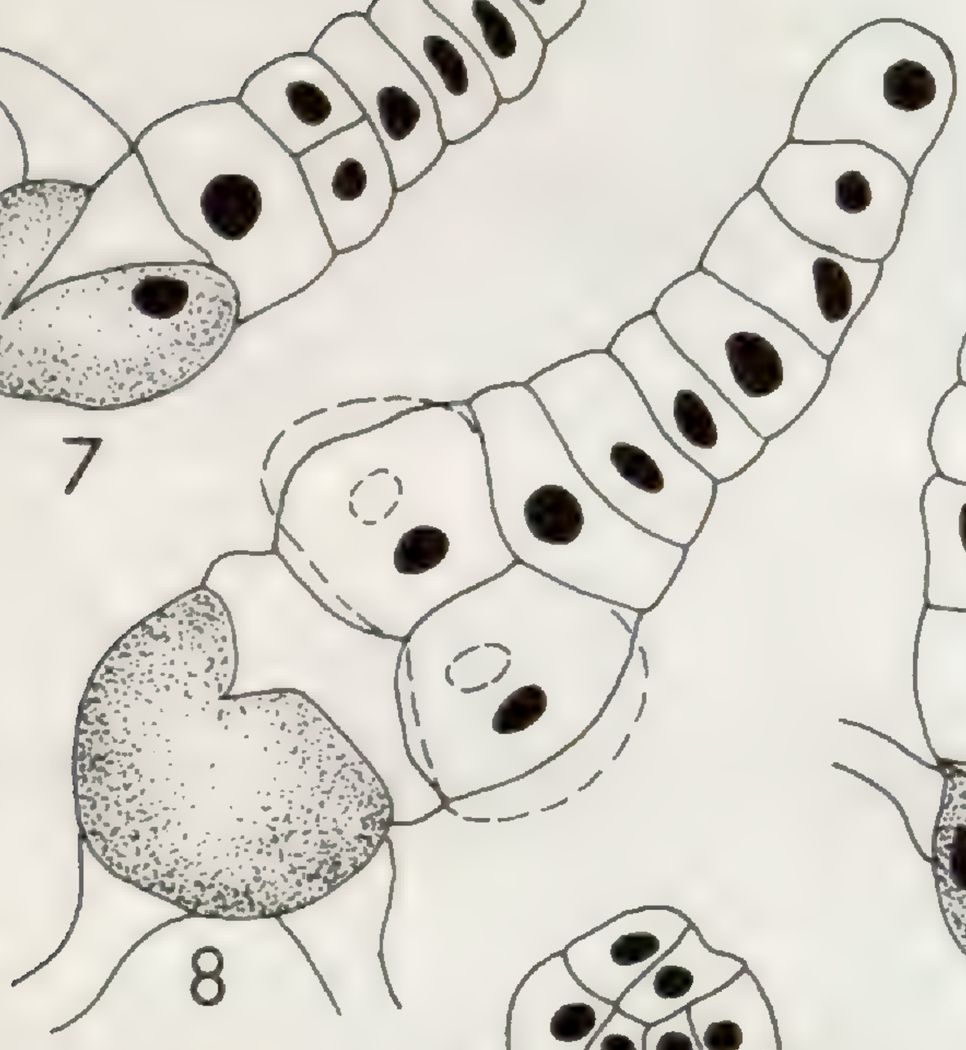
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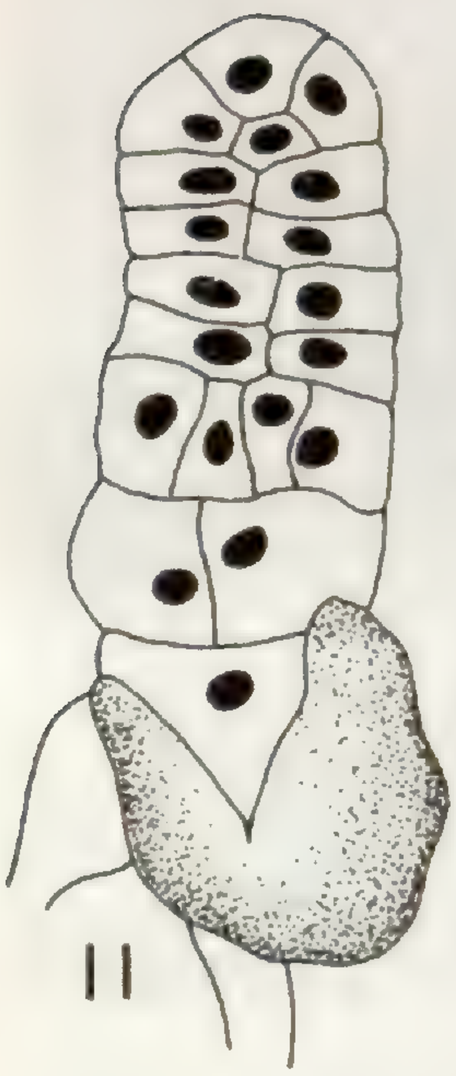
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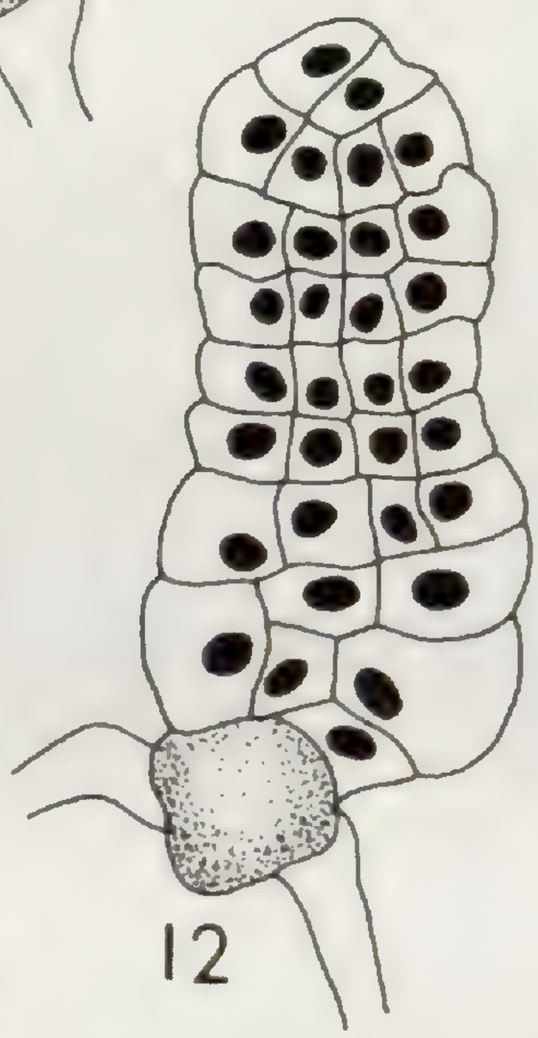
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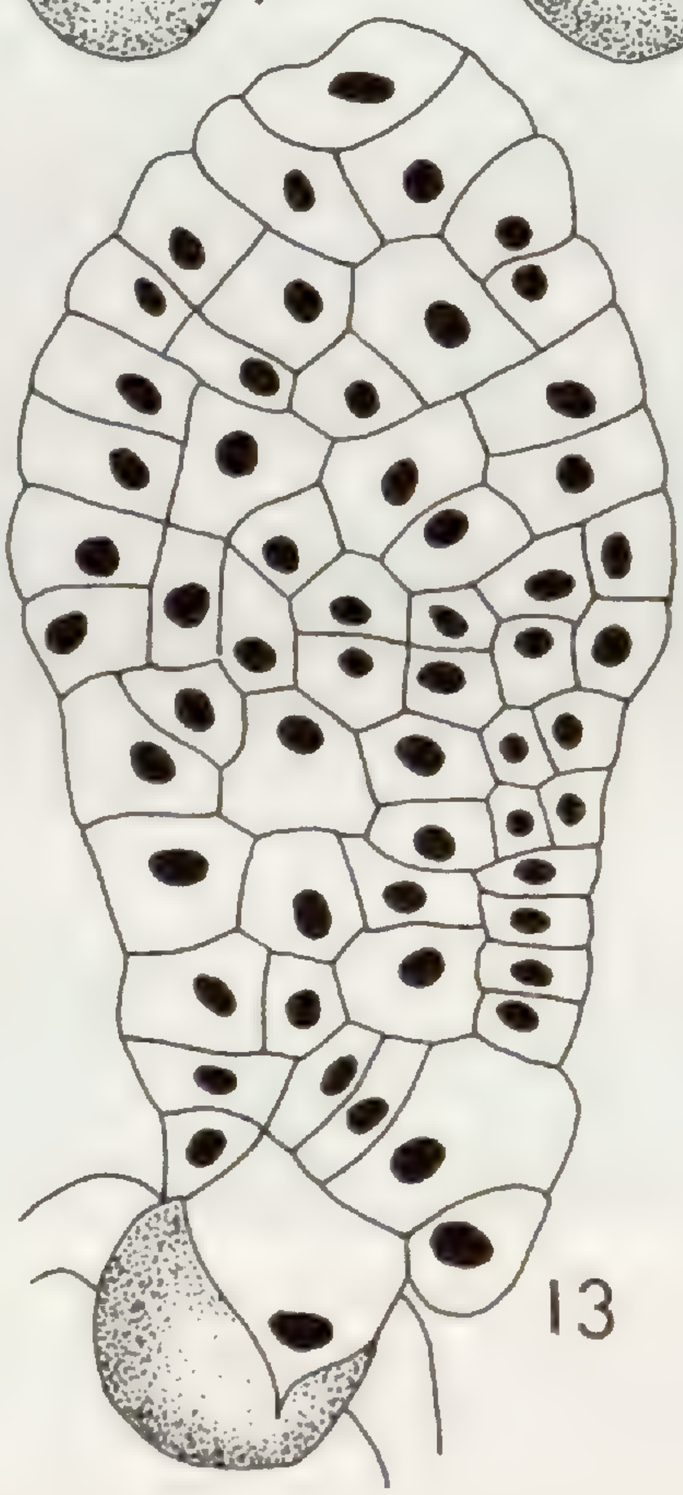
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spatulate gametophyte 4–6 cells wide (*Figs. 11–13*). About 17 days following sowing, the notch meristem can be seen along one of the lateral margins near the base of the two-dimensional filament (*Fig. 13*). With increasing growth of the gametophyte, a highly irregular, asymmetrical, more or less ovate prothallus is produced which bears a cushion (*Figs. 14–16*).

Older gametophytes may produce symmetrical wings on both sides of the meristem, and thus appear to have an apical notch. Wing tissue does not develop much beyond the notch, and the latter structure remains relatively shallow (*Figs. 17* and *18*).

Sexual maturity is reached quite rapidly in densely sown agar cultures. Sex organs can appear as soon as 23 days following sowing (*Table 1*). In the majority of plants studied, archegonia appeared before antheridia, although the unisexual archegoniate stage usually is very short and lasts only 1–3 days before hermaphroditism occurs. In some cultures (such as 123-A) initially male gametophytes were produced concurrently with initially female and hermaphroditic gametophytes. In culture 125, male gametophytes were never observed, and in nearly all other cultures their percentage of occurrence remained low. In culture 124, gametophytes expressed a sexual ontogeny which was initially male, female, and hermaphroditic, with a high percentage of antheridiate gametophytes. As the culture aged, the percentage of male gametophytes increased and the percentage of female gametophytes decreased, whereas the percentage of hermaphroditic gametophytes initially increased and then remained relatively constant (*Table 1*).

In soil culture, attainment of sexual maturity is somewhat delayed. In densely sown soil cultures, male gametophytes in all cultures are produced concurrently with female and hermaphroditic gametophytes and in significantly higher percentages than in dense agar cultures (*Table 2*). Under these conditions it appears that the species initially expresses a trigametophytic system.

In all gametophytes observed, archegonial necks are oriented either posteriorly toward the rhizoids or laterally toward the wings. Antheridia are initially produced near the notch and on the wing tissue in the immediate vicinity of the notch. In more mature gametophytes (*Fig. 18*), archegonia are numerous along the cushion of the gametophyte and antheridia are found on both wings bordering the cushion, to a lesser extent among the rhizoids near the base of the prothallus, and on the cushion itself. In some male gametophytes antheridia commonly are found throughout the cushion region.

Analysis of the above data pertaining to sex organ initiation indicates that under varying experimental conditions different percentages of male, female, and hermaphroditic gametophytes are initially expressed. In view of the importance that

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FIGS. 4–13. Gametophyte development of *A. danaeifolium*. FIG. 4. Three-celled gametophyte showing initial germination. FIG. 5. Initiation of one-dimensional filament. FIG. 6. One-dimensional filament. FIG. 7. Initiation of two-dimensional growth. FIG. 8. Three-dimensional gametophyte with four cells immediately above the basal cell. FIG. 9. Subsequent cell-divisions in two-dimensional filament. FIG. 10. Two-ranked cells in filament. FIGS. 11, 12. Two-dimensional prothalli 15 days after sowing. FIG. 13. Broadly spatulate prothallus 17 days after sowing, showing meristematic region along basal right hand margin.

TABLE 1. SEXUAL ONTOGENY IN DENSE AGAR CULTURES (30–60 prothalli/cm²).[1]

Days from sowing	*Sexual expression (%)*			
	Neuter	*Male*	*Female*	*Hermaphroditic*
		Culture No. 123-A		
24	6.7	13.3	26.7	53.3
27	13.3		26.7	60.0
30			25.0	75.0
33			12.0	88.0
36				100.0
44				100.0
		Culture No. 123-B		
23	95.0	5.0		
26	70.0		30.0	
29	38.5		11.5	50.0
32	19.0		23.8	57.1
35	10.5	5.3	10.5	73.7
38	4.8		52.4	42.8
54				100.0
		Culture No. 123-C		
23	100.0			
26	42.1		42.1	5.3
29	17.8		21.4	60.7
32	20.0		20.0	60.0
35	13.6		36.4	50.0
38	25.0		10.0	65.0
54	7.7	7.7		84.6
		Culture No. 124		
24	38.1	38.1	19.0	4.8
27	26.7	33.3	6.7	33.3
30	45.2	25.8	3.2	25.8
33	32.4	35.3	8.8	23.5
39	16.7	45.8	4.0	33.3
43	8.7	21.7	8.7	60.0
60	7.0	65.1	2.3	25.6
		Culture No. 125		
27	33.3		66.6	
30			40.0	60.0
33			40.0	60.0
36			25.0	75.0
		Culture No. 126-A		
25	33.3		60.0	6.7
30	32.0		52.0	16.0
33	23.8		23.8	52.4
36	9.5		14.3	76.4
44			21.7	78.3
60	13.3	6.7		80.0
		Culture No. 126-B		
27	26.7		40.0	33.3
30	31.6		15.8	52.6
33			33.3	66.7
36			35.0	65.0
44			15.0	85.0
60				100.0

[1]Each culture represents spore families from single parental sporophytes.

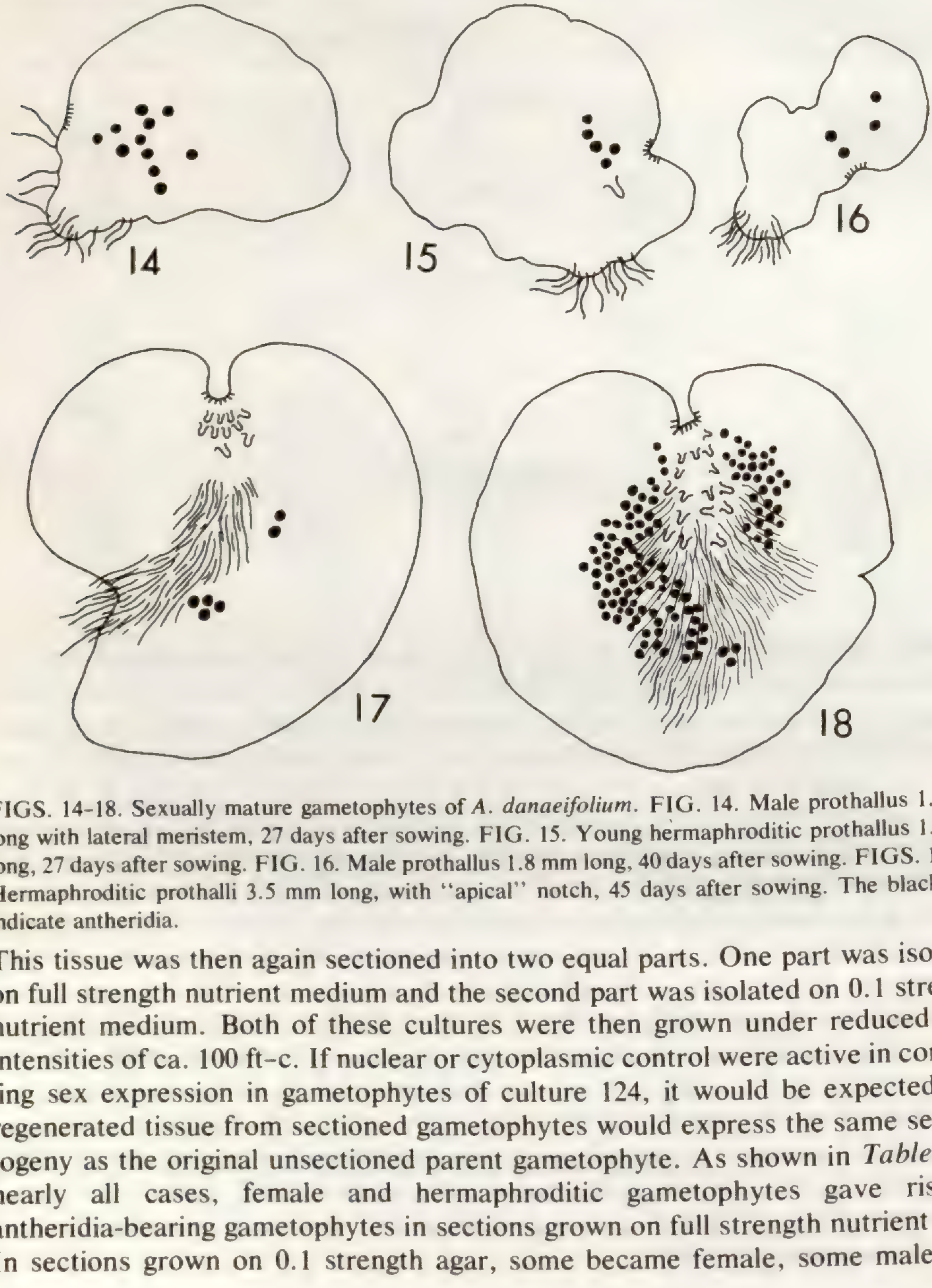
sex ontogeny has to mating systems in pteridophytes, a series of experiments was initiated to test various parameters of gametophyte biology in order to determine the cause of this variation. Culture 124 was selected for intensive study due to its significantly higher percentage of male gametophytes in both densely sown agar and soil cultures.

TABLE 2. SEXUAL ONTOGENY IN DENSE SOIL CULTURES (30–75 prothalli/cm^2).

Days from sowing	*Sexual expression (%)*			
	Neuter	*Male*	*Female*	*Hermaphroditic*
		Culture No. 123-A		
49	51.9	18.5	14.8	14.8
64	15.4	15.4	7.7	61.5
		Culture No. 123-B		
49	16.7	41.0	8.3	33.3
64		25.0	12.5	62.5
		Culture No. 123-C		
49	57.1	4.8	38.1	
64	33.3	11.1	44.5	11.1
		Culture No. 124		
45	30.5	60.9	4.3	4.3
49	41.2	41.2	5.9	11.7
91	4.3	60.9	13.0	21.8
		Culture No. 126-A		
45	42.1	5.3	26.3	26.3
49	23.1	7.7	23.1	46.1
64	25.0	8.3	25.0	41.7

There are several known factors which relate to the production of and the precocious initiation of antheridia in fern gametophytes. These include normal ontogenetic processes, incipient heterospory, antheridogen, nuclear or cytoplasmic inheritance, metabolic by-products, and gametophytic growth-rate. To test incipient heterospory and nuclear and cytoplasmic inheritance of sex, spore sizes were initially measured and monospore cultures (one gametophyte per culture dish) were established for 124 and 126-A. In both, spore sizes were unimodally distributed. Monospore cultures of gametophytes of 126-A expressed a sex ontogeny from initially female to hermaphroditic with the initial female period lasting about four days (*Table 3*). This ontogeny was essentially similar to that expressed in densely sown agar cultures (*Table 1*). In culture 126-A, some male gametophytes were produced after 36 days of growth. In culture 124, in monospore culture, gametophyte ontogeny is initially hermaphroditic. After 37 days of culture, 75% of the prothalli are hermaphroditic, 7.1% are male, and 3.6% are female. In gametophytes of this sporophyte, there is a significant difference between sex ontogeny in monospore culture with that expressed in densely sown composite cultures. In the latter, gametophytes are initially male or female or hermaphroditic and after 39 days of growth 45.8% of the culture is composed of male gametophytes (*Table 1*).

Because male, female, and hermaphroditic gametophytes developed in monospore culture in culture 124, further testing of sex inheritance in gametophytes of this sporophyte utilized sectioning techniques. In this experiment, gametophytes were initially grown in composite culture. When they were in early stages of becoming sexually mature, individual gametophytes were selected at random and wing tissue, which did not bear any sex organs, was sectioned off.



FIGS. 14–18. Sexually mature gametophytes of *A. danaeifolium*. FIG. 14. Male prothallus 1.5 mm long with lateral meristem, 27 days after sowing. FIG. 15. Young hermaphroditic prothallus 1.4 mm long, 27 days after sowing. FIG. 16. Male prothallus 1.8 mm long, 40 days after sowing. FIGS. 17, 18. Hermaphroditic prothalli 3.5 mm long, with "apical" notch, 45 days after sowing. The black dots indicate antheridia.

This tissue was then again sectioned into two equal parts. One part was isolated on full strength nutrient medium and the second part was isolated on 0.1 strength nutrient medium. Both of these cultures were then grown under reduced light intensities of ca. 100 ft–c. If nuclear or cytoplasmic control were active in controlling sex expression in gametophytes of culture 124, it would be expected that regenerated tissue from sectioned gametophytes would express the same sex ontogeny as the original unsectioned parent gametophyte. As shown in *Table 4*, in nearly all cases, female and hermaphroditic gametophytes gave rise to antheridia-bearing gametophytes in sections grown on full strength nutrient agar. In sections grown on 0.1 strength agar, some became female, some male, and

some hermaphroditic. It is assumed from these data, therefore, that factors other than nuclear and cytoplasmic inheritance are the primary determinants of sex in culture 124.

The remaining factors which are known to cause precocious antheridium production in ferns are antheridogens, which have been documented in a number of

TABLE 3. SEXUAL ONTOGENY IN ISOLATED AND UNCROWDED AGAR CULTURES.

Days from sowing	*Sexual expression (%)* *Neuter*	*Male*	*Female*	*Hermaphroditic*
	Culture No. 124, monospore			
21	100.0			
25	100.0			20.0
29	80.0			75.0
37	14.3	7.1	3.6	
	Culture No. 124, uncrowded (3–8 prothalli/cm²)			
40	5.0		5.0	90.0
	Culture No. 126-A, monospore			
26	40.0		60.0	
30	30.0		60.0	10.0
33			44.4	55.6
36	10.0	5.0	50.0	35.0
44				100.0

TABLE 4. SEX EXPRESSION FROM REGENERATED GAMETOPHYTE TISSUE AFTER 27 DAYS OF REGENERATED GROWTH, SEVEN REPLICATES FROM CULTURE 124.[1]

Sex of original prothallus before sectioning	*Regenerative sex expression* *Full strength nutrient medium*	*0.1 strength nutrient medium*
Immature female	male (numerous)	hermaphroditic (few ♀) (numerous ♂)
Hermaphroditic	male (few)	——[2]
Immature female	asexual	——[2]
Immature hermaphroditic	male (numerous)	female (with 5 archegonia)
Immature hermaphroditic	male (numerous)	hermaphroditic (both gametangia numerous)
Immature hermaphroditic	male (numerous)	male (numerous)
Immature hermaphroditic	male (numerous)	male (numerous)

[1]Grown under reduced light intensities of ca. 100 ft-c.

[2]Gametophyte tissue did not regenerate.

species (Voeller, 1964), metabolic by-products, and growth rates. The presence of an antheridogen in culture 124 was tested by growing a composite culture of gametophytes in a 100 × 15 petri dish containing nutrient agar, removing the gametophytes following the attainment of sexual maturity, transferring a block of agar from this dish and placing it on top of a fresh solidified nutrient agar in which no gametophytes had been grown. Spores were then resown on top of the agar

block and new agar and gametophytes were analyzed for sex ontogeny. In addition, uncrowded cultures were established (3–8 prothalli/cm^2) and sex ontogeny was observed. Antheridogens have been found to be active in extremely small concentrations. They are hypothesized to be secreted into the medium by early germinating spores or by meristematic gametophytes and to cause later germinating spores and gametophytes and slower growing gametophytes to produce antheridia precociously. If antheridogen were being produced in culture 124, gametophytes growing on a substrate on which a previous gametophyte popula-

TABLE 5. SEX ONTOGENY ON RESOWN AGAR BLOCKS AND ON FRESH AGAR ADJACENT, CULTURE 124.

Days from sowing	*Sexual expression (%)* *Neuter*	*Male*	*Female*	*Hermaphroditic*
	Prothalli on agar blocks			
17	100.0			
21	91.7	8.3		
25	95.7		4.3	
29	80.0	5.0	15.0	
33	37.5	12.5	20.0	30.0
42	22.0	36.0	2.0	40.0
	Prothalli immediately adjacent to agar blocks			
29	84.4	12.5	3.1	
33	46.3	18.5	7.4	27.8
42	17.1	39.0	4.9	39.0
	Prothalli distant from agar blocks			
33	51.3	17.9	12.9	17.9
42	10.7	53.6		35.7

tion had been grown would be expected to produce a large percentage of male gametophytes. In addition, under lightly sown conditions the frequency of male gametophytes should be increased over that of the monospore culture. Results are given in *Tables 3* and *5*. On the resown agar block, male gametophytes are initially produced four days before female gametophytes and 12 days before hermaphroditic gametophytes. However, the percentage of male gametophytes is low and remains low. After 33 days of growth, there are fewer male gametophytes on the resown block than on either the fresh agar or in the original densely sown agar culture (*Table 1*). In addition, gametophytes grown under low densities express no male gametophytes after 40 days of growth (*Table 3*).

Although the results of the experiments performed here do not definitely disprove an antheridogen in culture 124, we do not believe that one exists. If there is an antheridogen, it does not react in the same manner as that of other species which have been reported, as in *Ceratopteris* (Schedlbauer & Klekowski, 1972). In addition, other plants of the species investigated here indicate no signs, especially in composite culture, of an antheridium-inducing substance.

If antheridogen is not present in culture 124, other factors such as metabolic by-products or growth rates must be responsible for the production of increased numbers of male gametophytes in composite culture in culture 124. In all plants tested on soil cultures, where growth rates are reduced, a significant increase in male gametophytes was observed (*Table 2*). In addition, in culture 124, there is a

direct correlation between gametophyte size and sex ontogeny (*Table 6*). In uncrowded culture (3–8 gametophytes/cm^2), mean gametophyte size after 39 days of growth was significantly higher than in all other cultures observed. Under these conditions no male gametophytes are produced. Under other conditions, male gametophytes are produced, with the most frequent occurrence being under those conditions which produce the smallest mean gametophyte size (on soil and in higher density resown agar cultures). Therefore, it appears that decreased growth rate in *Acrostichum* is the primary determinant of precocious antheridium production. In addition, it appears that culture 124 also produces some non-antheridogen metabolite which is secreted into the medium, which affects growth rate to a limited extent, thereby increasing antheridium production.

Parameters of gametophyte morphology and physiology as discussed above yield information concerning the probabilities of intragametophytic or intergametophytic mating in *A. danaeifolium*. Factors of the gametophyte generation which appear to increase the probability of intergametophytic mating include the production of both male and female gametophytes especially under soil culture. However, in some cases, gametophytes initially become hermaphroditic or initially produce antheridia, thus increasing the probability of intragametophytic selfing. In addition, the placement of antheridia in close proximity to the archegonial necks has been interpreted as favoring self-fertilization.

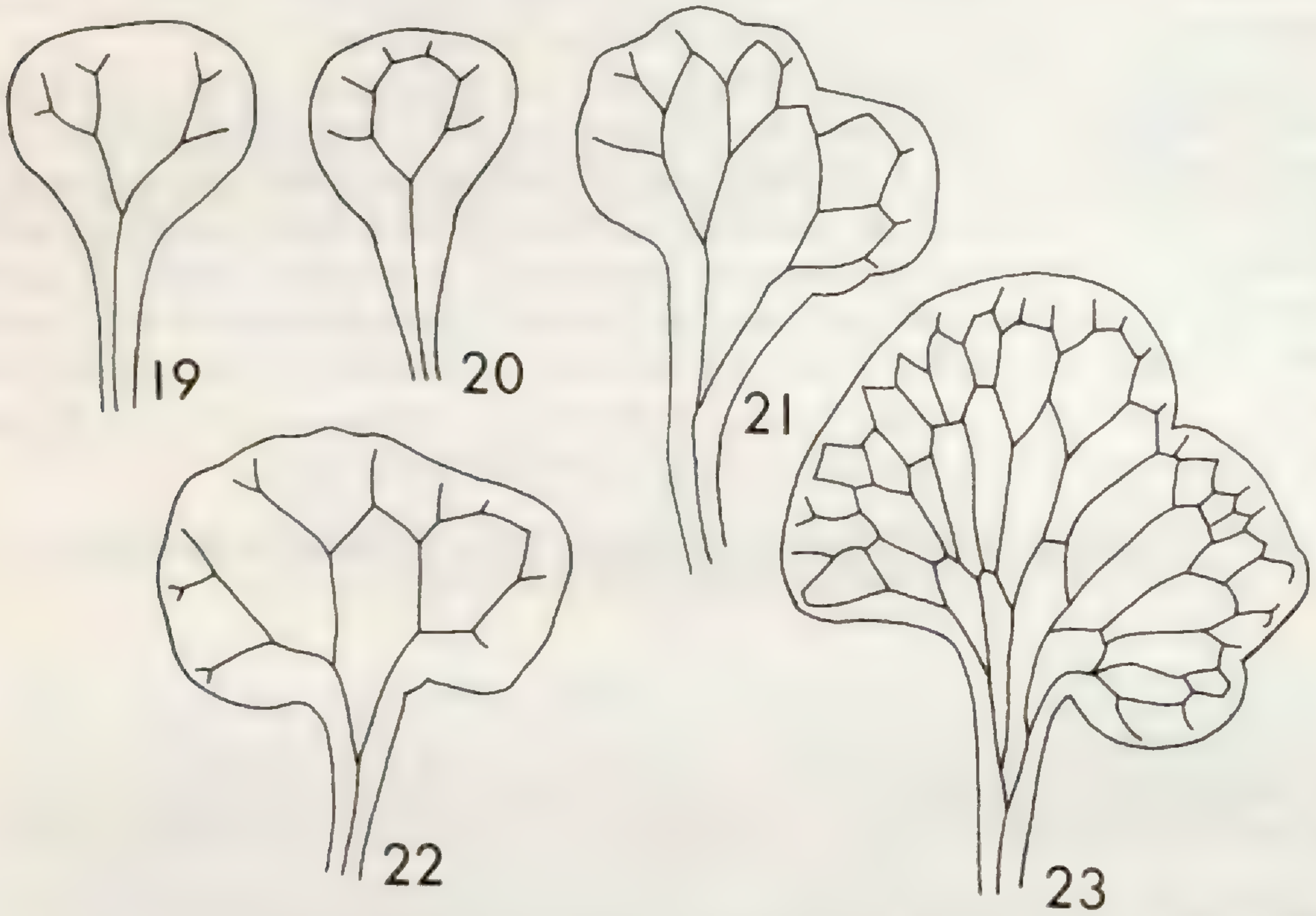
TABLE 6. GAMETOPHYTE SIZE RELATIVE TO SOWING DENSITIES AND SUBSTRATE, CULTURE 124.

Density (prothalli/cm^2)	*Days from sowing*	*Substrate*	*Gametophyte size (mm^2)* *Range*	*Mean*
Monospore	36	agar	4.48–12.25	7.79
3–8 (mean = 4)	39	agar	0.54–24.48	9.62
30–60 (mean = 46)	36	resown agar	0.06– 6.09	1.83
30–75 (mean = 53)	45	soil	0.09–11.10	2.15

Additional information relative to the reproductive biology can be obtained from an analysis of genetic load in sporophytes. The screening of sporophytes for recessive deleterious genes is easily accomplished by isolating 25 or more hermaphroditic prothalli and allowing intragametophytic selfing to occur. As gametes from a single prothallus can be considered to be genetically identical, recessive deleterious genes should be expressed in resultant zygotes or sporophytes. Sporophytes which express heterozygosity for genetic load in their gametophytes must therefore be heterozygous and are assumed to have resulted from intergametophytic mating (assuming homologous chromosome pairing). The presence of genetic load is also supportive of intergametophytic mating because it tends to eliminate products of intragametophytic selfing. Sporophytes having no genetic load have a higher probability of being genetically homozygous and of originating from intragametophytic selfing. However, it must be stated that because we do not know how genetic load is inherited in ferns and because it has not been possible to experimentally test our hypotheses, all of the above statements are subject to verification.

To analyze the frequency of recessive deleterious genes in *A. danaeifolium*, 25 gametophytes per sporophyte (= a gametophyte family) were selected at random from stock cultures and individually isolated before the attainment of sexual maturity in 60 × 15 mm petri dishes containing nutrient agar. The cultures were watered periodically to facilitate fertilization. Resultant sporophytes were allowed to develop to the third frond stage. Results of these studies are given in *Table 7*.

Genetic load was determined as the percent of hermaphroditic gametophytes per gametophyte family which failed to yield normal viable sporophytes. Expressions of genetic load took the form of zygotic lethals (in 0.6% of the 175 gametophytes tested), embryonic lethals (in 5.7% of the gametophytes tested), and later sporophytic lethals (in 4.0% of the gametophytes tested). Results of the breeding tests indicate that three of the seven sporophytes tested were completely devoid of genetic load. In those sporophytes expressing load, it varied from 4.0% in culture 126-A to 32.0% in culture 124. The mean genetic load for all plants was 10.3%.



FIGS. 19-23. Early sequential frond development in *A. danaeifolium*. FIGS. 19-21. First fronds, 2.7 mm, 2.0 mm, and 5.1 mm wide, respectively. FIGS. 22, 23. Second fronds, 9 mm and 13 mm wide, respectively.

Deleterious genotypes were expressed with greatest frequency either as embryonic lethals in 42.8% of the sporophytes, or later sporophytic lethals, in 28.6% of the sporophytes. Zygotic lethals were rare.

It appears that different expressions of lethality in different combinations occur in different gametophyte families. Therefore, separate genetic factors are probably responsible for the different expressions in the various families.

Cross tests were devised to document the genetic basis for the lack of sporophyte production in isolate culture. In these tests, a pair of gametophytes, one from each of two sporophytes, were placed in a single 60 × 15 mm petri dish containing nutrient agar. Twenty to 30 prothalli from each sporophyte were tested in this manner. Cultures were watered periodically to insure fertilization. It is assumed that if non-genetic factors are responsible for the lack of sporophyte

TABLE 7. FREQUENCY OF DELETERIOUS SPOROPHYTIC GENOTYPES IN INTRAGAMETOPHYTICALLY SELFED, ISOLATED, HERMAPHRODITIC GAMETOPHYTES.

	Parental sporophytes							
	123-A	*123-B*	*123-C*	*124*	*125*	*126-A*	*126-B*	*Means (%)*
Number (%) of normal sporophytes[1]	22 (88)	25 (100)	19 (76)	17 (68)	25 (100)	24 (96)	25 (100)	89.7
Number (%) not producing sporophytes[1]	3 (12)		6 (24)	2 (8)				6.3
Later sporophytic deleterious genotypes				6 (24)		1 (4)		4.0
Embryonic lethal genotypes	3		5	2				5.7
Zygotic lethals			1					0.6
Total lethal & deleterious genotypes	3		6	8		1		10.3
Number (mean) visible lethal embryos per prothallus	4–14 (7.1)		0–24 (8.0)	6–7 (6.5)				

[1]Based on 25 isolated prothalli from each parental sporophyte.

production in the isolates then at least some of the prothalli in the cross tests would fail to yield sporophytes (barring lethal dominant mutations). In all cross tests (which involved sampling at least 20 prothalli of the following cultures: 123-A × 125, 123-A × 123-C, 123-B × 126-B, 123-C × 126-B, and 126-A × 124), all gametophytes yielded 100% viable, normal sporophytes. It is concluded, therefore, that the lack of sporophyte production and the deleterious gene expression in the isolated gametophytes was due to the genotypes that these gametophytes possessed which were lethal or semi-lethal in the homozygous sporophyte generation.

DISCUSSION

Gametophyte Morphology.—In most respects the gametophyte ontogeny of *A. danaeifolium* reported here agrees with that reported for *A. speciosum* Willd. (Stokey & Atkinson, 1952), an Austral-Asian segregate of *A. aureum* L. of questionable status. Qualitative characteristics which are similar include spore size and shape, germination, formation of the one-dimensional filament, formation of the lateral meristem, antheridium and archegonium structure, and lack of trichomes on the prothallus. In *A. speciosum*, Stokey and Atkinson report that two-dimensional growth is usually initiated by longitudinal or occasionally transverse divisions in the second or third cell back from the terminal cell of the one-dimensional filament. In *A. danaeifolium*, two-dimensional growth was usually initiated by longitudinal divisions in more basally located cells, although infrequently it was initiated by cells in a more apical position. A second difference noted was in the cells most actively contributing to the two-dimensional gametophyte. In *A. speciosum*, the third cell from the tip appears to be most active in contributing to the formation of a two-dimensional plate, which leads to a spatulate structure which is six or more cells broad near the tip and only one or two cells broad near the base. In *A. danaeifolium*, nearly all but the basal and sub-basal cells of the one-dimensional filament contribute to the formation of the two-dimensional plate, which is nearly as broad at the base as it is near the tip.

Other more quantitative differences can be noted, but these are more highly susceptible to culture conditions. Specifically, *A. speciosum* antheridia appear 42–49 days after sowing, and there may be as many as 15 or 20 produced before archegonia appear. Archegonia appear in 63–70 days. In *A. danaeifolium*, antheridia and archegonia production is variable, but usually occurs much earlier.

The results of these studies are insufficient to indicate whether gametophyte characteristics provide information pertaining to delimitation of species boundaries in *Acrostichum*. More specific studies are needed from plants from diverse habitats and geographical areas, with both wild material as well as material cultured under a common regime to determine the extent of genetic control of the differing features.

Reproductive Biology.—In nearly all cultures of *A. danaeifolium* examined, initial sex ontogeny was either from female to hermaphroditic, initially dioecious, or a trigametophytic system with male, female, and hermaphroditic gametophytes. In other species which have been investigated, these types of sex ontogeny have been correlated with intergametophytic mating and usually are related to measurable levels of heterozygosity for genetic load, as in *Cibotium glaucum* (Lloyd, 1974b), *Onoclea sensibilis* (Saus & Lloyd, 1976), and *Stenochlaena tenuifolia* (Klekowski, 1970c). However, in *A. danaeifolium* 42.8% of the sporophytes tested were devoid of measurable load to the third frond stage of sporophyte development in young homozygotes, and 28.6% expressed levels of 12% or less. Close examination of sex ontogeny and other features of the biology of *Acrostichum* indicate several reasons why such low levels of genetic load (implying frequent intragametophytic mating) are expressed. For example, culture

124 expressed the highest level of load of all sporophytes tested (32%). Gametophytes from this sporophyte produce a population which is initially dioecious and later male and hermaphroditic with few females. This type of population system initially has a high probability of intergametophytic mating. In other sporophytes with higher load levels, a bigametophytic or trigametophytic system is initially expressed, or the unisexual archegoniate stage is extended up to eight days or more before hermaphroditism occurs. In these latter situations, there are ample opportunities for intergametophytic mating to occur initially. In those sporophytes expressing no genetic load, gametophyte populations are initially female and hermaphroditic, initially female, or initially male (with these becoming hermaphroditic and female very shortly). In all of these, the length of the unisexual archegoniate stage before the attainment of hermaphroditism is less than three days, thereby decreasing the probability of intergametophytic mating.

Other factors also relate to increasing the probability of intragametophytic mating in *Acrostichum*. For example, the close proximity of antheridia to archegonial necks encourages self-fertilization, especially if there is little or no genetic load to eliminate the products of such fertilizations. In addition, the production of massive numbers of spores by fertile sporophylls would tend to increase the probability of intergametophytic selfing (inbreeding), thus decreasing heterozygosity and further eliminating recessive deleterious genes.

It is interesting to compare the reproductive biology and genetic load of *A. danaeifolium* with that of *Ceratopteris thalictroides*, another aquatic or semi-aquatic species of homosporous ferns which has been studied intensively (Klekowski, 1970b). Both species are characterized by rapid gametophyte growth and early attainment of sexual maturity. Although both species present gametophyte population structures which might tend to favor intergametophytic mating, those populations which have been investigated indicate that heterozygosity for recessive deleterious genes is low or absent (in recent studies of *A. danaeifolium* from Florida and Puerto Rico and *A. aureum* from Florida, results similar to those expressed by Mexican *A. danaeifolium* were obtained). Other than those reproductive features mentioned above, the species are highly dissimilar in most other characteristics. For example, *Ceratopteris* produces relatively few spores per plant compared to *Acrostichum*, but has capabilities for highly effective vegetative reproduction (Lloyd, 1973). Results of these studies suggest that the aquatic habitat is selecting for rapid gametophyte maturation and that this, in turn, is perhaps responsible for the increased levels of intragametophytic mating and the elimination of recessive deleterious genes.

It should be emphasized that the cultural regimes utilized in these experiments are not representative of the natural habitat of the species. Further testing of the hypotheses set forth above is required, primarily with an ecological study of the gametophyte generation in nature.

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Larry L. Kiefer (1935–1975)

Larry Kiefer was born in Wichita, Kansas on May 7, 1935. During his high school years he developed an interest in ferns, and in subsequent years he collected them in Kansas, Arkansas, Colorado, and Utah. He studied music, specializing in voice, graduated from Wichita State University in 1957, and then taught music for a time. When he moved to California in 1963, it was natural for him to continue his interest in ferns. He became a social worker for the County of Los Angeles, but also called himself a quasi-professional musician and kept an active interest in music.

Larry's deep interest in plants, discerning eye, and keen mind could have made him an excellent professional botanist. He had a perceptive understanding of California ferns and their distribution. He was an indefatigable hiker and traversed many miles on foot into remote areas in search of ferns. Although his collecting centered in southern California, he also collected from Baja California to the state of Washington. Larry was always willing to help researchers, and made special trips to locate specimens for their work. This brought him into

contact with many renowned botanists. Through their generous help and his own efforts he compiled detailed information on the localities and distributions of California ferns, which was useful to other botanists in preparing and updating various manuals and Floras. Larry was the senior author of the "Check List of California Pteridophytes" (Madroño **19:** 65–73. 1967).

Larry had been in ailing health and died in a fall on May 18, 1975. He leaves his parents, Orvel and Eva Kiefer (the former Miss Eva Williams) of Wichita, Kansas, and a brother, James Kiefer of Olivehain, California. Plans are underway to establish a memorial to Larry. Also in his memory his family has donated his herbarium to the University of California at Los Angeles. Students and researchers will find his carefully prepared specimens an invaluable help in their work. Professional and amateur pteridologists will miss Larry Kiefer and his knowledge of California pteridophytes very much.—*Barbara Joe Hoshizaki, Life Science Department, Los Angeles City College, Los Angeles, CA 90029.*

REVIEW

"PTERIDOLOGY 1947–1972," by W. H. Wagner, Jr. Ann. Missouri Bot. Gard. **61:** 86–111. 1974.—Did you know that some fern spores contain chlorophyll? That some gametophytes live an independent existence and spread by means of prothallial gemmae and that at least one of these (the Shoestring Fern, *Vittaria*) never produces sporophytes; that one species of the typically tropical genus *Hymenophyllum* has been found in Alaska? Did you know that *Polypodium dispersum*, which ranges from Florida to Bolivia, undergoes no change in chromosome number during its life cycle and that its gametophyte simply transforms into a sporophyte? That the entire annulus of *Negripteris scioana* consists of cells that have undifferentiated, corky walls? That the diploid chromosome number in *Ophioglossum* has been found to exceed 1,200?

All of these findings in fern study during the past 25 years are noted in Dr. Wagner's highly readable review of recent pteridology. His summary of a quarter century of accomplishment in our field updates the review of pteridology by Irene Manton in E. L. Kessel's "A Century of Progress in the Natural Sciences" (1955) and the important summaries by Pichi Sermolli in O. Hedberg's "Systematics of Today" (1958) and by Rolla Tryon in J. Ewan's "A Short History of Botany in the United States" (1969).

Other points that Wagner discusses include: homosporous lycosphens show chromosomes with high base numbers (x=20–50), but heterosporous ferns have lower numbers; the sporangium of *Platyzoma* contains spores of two sizes: 16 large ones produce archegonial prothalli and 32 small ones produce antheridial prothalli; Bower's classic "phyletic slide" of sori moving from the frond margin to its back during evolutionary history actually may have occurred both away from and towards the margin in primitive ferns; five different types of stomata have

been recognized in the 250 fern genera examined; and a dramatic range extension of the tropical *Grammitis nimbata* has been found—it occurs as an independent gametophyte with a few, imperfect sporophytes in the mountains of North Carolina, 900 miles north of its usual range. Think of the implications the latter discovery carries for the past history of the pteridophytes in their interaction with the great climatic changes that have swept over North America.

One of the many results of cytogenetic investigations is the systematic position of genera, whether they will continue to be accorded full generic status or be subsumed (Wagner's word) into larger genera. For example, the genera *Camptosorus, Ceterach,* and *Phyllitis* would be subsumed under *Asplenium*.

Of the 224 titles listed in Wagner's selected bibliography as contributed in the last 25 years, the largest number (20) were published by C. V. Morton; next, Wagner had 18; and R. M. Tryon had 15. Over 36 major revisions and monographs have appeared in the last quarter century. The sum is tallied in the largest question: "What contributions can the unique features of pteridophytes make to the understanding of basic biological phenomena?"—*Joseph Ewan, Department of Botany, Tulane University, New Orleans, LA 70118.*

AMERICAN FERN JOURNAL

Manuscripts submitted to the JOURNAL are reviewed for scientific content by one or more of the editors and, often, by one or more outside reviewers as well. During the past year we have received the kind assistance of Drs. R. H. Eyde, R. M. Lloyd, J. M. Mitchell, J. Nowicke, L. Pike, W. Shropshire, A. R. Smith, R. G. Stolze, W. H. Wagner, Jr., R. A. White, D. P. Whittier, and J. J. Wurdack. We welcome suggestions of other reviewers and offers of assistance.—D.B.L.

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P. 86, line 12. For "is not" read "possibly is not."

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P. 99, line 23. For "Fresno" read "Trinity."

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